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BULLETIN OF
THE BRITISH MUSEUM
(NATURAL HISTORY)

ZOOLOGY

Vol. 20

1970-1971

BRITISH MUSEUM (NATURAL HISTORY)
LONDON: 1975



DATES OF PUBLICATION OF THE PARTS

No. 1	.	.	.	.	.	18 August 1970
No. 2	.	.	.	.	.	9 November 1970
No. 3	.	.	.	.	.	20 January 1971
No. 4	.	.	.	.	.	10 December 1970
No. 5	.	.	.	.	.	31 December 1970
No. 6	.	.	.	.	.	21 December 1970
No. 7	.	.	.	.	.	28 December 1970
No. 8	.	.	.	.	.	8 February 1971



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THE CLUPEOID FISHES
DESCRIBED BY STEINDACHNER



P. J. P. WHITEHEAD

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DESCRIBED BY STEINDACHNER

BY
PETER JAMES PALMER WHITEHEAD

Self



Pp. 1-46 ; 3 Plates, 4 Text-figures

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THE BULLETIN OF THE BRITISH MUSEUM
(NATURAL HISTORY), instituted in 1949, is
issued in five series corresponding to the Departments
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*This paper is Vol. 20 No. 1 of the Zoological series.
The abbreviated titles of periodicals cited follow those of
the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 18 August, 1970

*Price £1 9s.
(£1.45)*

THE CLUPEOID FISHES DESCRIBED BY STEINDACHNER

By P. J. P. WHITEHEAD

INTRODUCTION

MOST of the new fishes described by Franz Steindachner (1834-1919) are in the Naturhistorisches Museum in Vienna ; a few types and many duplicates are found in other museums. Steindachner's original descriptions and figures are usually excellent, often with far more detail than his contemporaries troubled to include, but modern studies have made a reassessment of his species urgent in certain groups. The opportunity is taken here to redescribe and discuss the types of Steindachner's 21 clupeoid fishes (1 Dussumieriidae, 12 Clupeidae, 8 Engraulidae—see Table 1).

Between 1859 and 1917, Steindachner produced nearly two hundred and fifty papers in which he described about a thousand new species of Recent fishes, 29 fossil species and a number of new reptiles and amphibians. Most of the specimens resulted from his participation in several expeditions, the most important in the present study being those to South America and West Africa.

As a student, Steindachner's legal studies had given way to an interest in natural history (and ichthyology in particular), largely through the encouragement of Eduard Suess. By 1857 Steindachner was a regular visitor to the Imperial natural history cabinet and in 1861 he accepted a permanent post there. One of his first tasks, suggested by Rudolf Kner, was to share with Giovanni Canestrini the study of the material brought back from the Novara Expedition of 1857-9. Determined to enlarge the Imperial collections, Steindachner made expeditions to Switzerland, southern Spain, Portugal and the Canary Islands and in 1868-9 he collected in Senegambia. Subsequently, he accepted Louis Agassiz's invitation to come to Cambridge (Massachusetts) to work on the Thayer material collected in Brazil in 1865-6. Granted leave of absence from Vienna, Steindachner joined Agassiz in March, 1870 and later agreed to accompany him on a collecting trip in the ship *Hassler* on a cruise down the Atlantic coast of the Americas and back up the Pacific coast to San Francisco, a voyage of nine months. For a further seven months Steindachner collected in the United States for the Vienna museum, before returning home.

Twenty-nine years were to elapse before he revisited South America, this time to the northeast provinces of Brazil. In the meantime he participated in and later led three of the Austrian deep-sea Mediterranean expeditions and two Red Sea expeditions, and the fish collections at Vienna grew at such an enormous rate that new accommodation was required. The transfer of the fish and reptile collections from the seven small and dark rooms of the Imperial Cabinet in Joseph Platz to the present museum building was completed by 1886 and the following year Steindachner was

appointed Director of the zoological collections with a suite of rooms which now houses the ichthyological collections. A full account of Steindachner's career has been given by Kähsbauer (1959).

Perusal of the modern fish collection shows to what extent it is indebted to Steindachner's efforts. Amongst the material, there are also Brazilian specimens collected by Johann Natterer (recognizable by red painted roman and arabic numerals on the backs of mounted skins), Japanese fishes (dried) from Burger (many still with paper glued to protect the fins), Red Sea fishes from Eduard Rüppell, type and other material relating to Rudolf Kner and Johann Heckel, and exchange specimens from Leyden, Paris, etc.

Kähsbauer (1959) gave a useful index of the new species described by Steindachner (a few species missing and some MS. names or already published names included).

The Steindachner types are not segregated from the non-typical material and are not always indicated as such ; in some cases a type indication relates merely to a MS. name. No peculiarities of labelling, type of bottle, marking of specimens, etc., were found which would aid in the recognition of types other than the dates given on the labels (which may in some cases refer to the date of incorporation and not to the date of collection).

For the 21 clupeoid species, types were not found for the following species :

Clupea rechingeri (= ? *Herklotsichthys punctatus*)

Clupea notacanthoides (= *Ethmidium maculatum notacanthoides*)

Engraulis nattereri (= *Anchoviella nattereri*)

Engraulis poeyi (= *Lycengraulis poeyi*)

The types of 2 species were reported by Steindachner (see under species) to be in Stuttgart :

Clupea macrolepis (SMNS. 2292)

Clupea neopilchardus (not found, see p. 16).

As an indication of Steindachner's general approach to ichthyology, his clupeoid species can be said to have been described accurately, usually at greater lengths than in contemporary descriptions, but with little or no attempt to explore affinities beyond those of immediate specific relationships. Initially, his clupeoid genera followed those of Valenciennes (1847, 1848), but he later tended to use the two compendium genera, *Clupea* and *Engraulis*, favoured by Günther (1868). Fourteen Steindachner names are here recognized as senior synonyms (Table 1).

The following abbreviations have been used :

S.L. standard length

tot.l. total length

g.r. gillrakers

NMV Naturhistorisches Museum, Vienna

SMNS Staatliches Museum für Naturkunde, Stuttgart

BMHN British Museum (Natural History), London

MNHN Museum National d'Histoire Naturelle, Paris

RMNH Rijksmuseum van Natuurlijke Historie, Leyden

ZMA Zoölogisch Museum, Amsterdam

ZMC Zoologisk Museum, Copenhagen

I am indebted to Dr. Paul Kähnsbauer for his kindly help during my visit to Vienna and for allowing me to borrow many types for further examination.

TABLE I

Clupeoid species described by Steindachner

<i>Steindachner name</i>	<i>Identification</i>
DUSSUMIERIIDAE	
1. <i>Alausa alburnus</i> Kner & Steind., 1866	<i>Spratelloides delicatulus</i> (Bennett, 1831)
CLUPEIDAE	
2. <i>Clupea rechingeri</i> Steind., 1908	? <i>Herklotsichthys punctatus</i> (Rüppell, 1837)
3. <i>Clupea brasiliensis</i> Steind., 1879	<i>Sardinella brasiliensis</i> (Steind., 1879)
4. <i>Clupea macrolepis</i> Steind., 1879	<i>Escualosa thoracata</i> (Val., 1847)
5. <i>Clupea amazonica</i> Steind., 1879	<i>Rhinosardinia amazonica</i> (Steind., 1879)
6. <i>Pellonula bahiensis</i> Steind., 1879	<i>Rhinosardinia bahiensis</i> (Steind., 1879)
7. <i>Alausa fimbriata</i> Kner & Steind., 1879	<i>Sardinops sagax sagax</i> (Jenyns, 1842)
8. <i>Clupea neopilchardus</i> Steind., 1879	<i>Sardinops sagax neopilchardus</i> (Steind., 1879)
9. <i>Clupea setosa</i> Steind., 1869	<i>Ethmalosa fimbriata</i> (Bowdich, 1825)
10. <i>Clupea notacanthoides</i> Steind., 1869	<i>Ethmidium maculatus notacanthoides</i> (Steind., 1869)
11. <i>Pellona furthii</i> Steind., 1875	<i>Ilisha furthii</i> (Steind., 1875)
12. <i>Pellona panamensis</i> Steind., 1875	<i>Ilisha furthii</i> (Steind., 1875)
[Pellona <i>staudingeri</i> , MS. name]	<i>Pellona flavipinnis</i> (Val., 1837)
[Pellona <i>macrolepis</i> , MS. name]	<i>Pellona flavipinnis</i> (Val., 1837)
13. <i>Pristigaster (Odontognathus) panamensis</i> Steind., 1876	<i>Odontognathus panamensis</i> (Steind., 1876)
ENGRAULIDAE	
14. <i>Engraulis vaillanti</i> Steind., 1908	<i>Anchoviella vaillanti</i> (Steind., 1908)
15. <i>Engraulis nattereri</i> Steind., 1879	<i>Anchoviella nattereri</i> (Steind., 1879)
16. <i>Engraulis januaria</i> Steind., 1879	<i>Anchoa januaria</i> (Steind., 1879)
17. <i>Engraulis nasus</i> Kner & Steind., 1866	<i>Anchoa nasus</i> (Kner & Steind., 1866)
18. <i>Engraulis peruanus</i> Steind., 1879	<i>Anchoa nasus</i> (Kner & Steind., 1866)
19. <i>Engraulis panamensis</i> Steind., 1875	<i>Anchoa panamensis</i> (Steind., 1875)
20. <i>Engraulis macropolepidotus</i> Kner & Steind., 1865	<i>Anchovia macropolepidota</i> (Kner & Steind., 1865)
21. <i>Engraulis poeyi</i> Kner & Steind., 1865	<i>Lycengraulis poeyi</i> (Kner & Steind., 1865)

Family **DUSSUMIERIIDAE**
SPRATTELLOIDES Bleeker, 1851

Spratelloides Bleeker, 1851, *Natuurk. Tijdschr. Ned. Ind.*, 2 : 214 (Type : *Clupea argyrotaeniata* Bleeker = *Clupea gracilis* Temminck & Schlegel).

In a recent revision of the genus (Whitehead, 1962) two species were recognized, *S. gracilis* (Temm. & Schl.) and *S. delicatulus* (Bennett). Subsequent studies have dealt with type specimens (Whitehead *et alii*, 1966 : 33-37), further differences between the two species (Whitehead, 1965 : figs. 2, 3; supra-maxillary shape, posterior frontal fontanelles) and distribution (Whitehead, 1969a).

1. *Alausa alburnus* Kner & Steind., 1866
 = *Spratelloides delicatulus* (Bennett, 1831)

(Plate 1a)

Clupea delicatula Bennett, 1831, *Proc. zool. Soc. London*, 1 : 168 (Mauritius).

Alausa alburnus Kner & Steindachner, 1866, *Sitzb. K. Akad. Wiss. Wien*, 54 : 387, pl. 1, fig. 16 ("Valparaiso"—in fact Samoa, see below).

LOCALITY. As pointed out by Günther (1909 : 384), the original reference number and the locality recorded for this species by Schmeltz (1869 : 25) in the catalogue of the Godeffroy Museum at Hamburg were attributed by Kner & Steindachner to *Alausa fimbriata*, and *vice versa*. The correct locality for *Alausa alburnus* is thus Samoa ; *Stolephorus delicatulus* is not recorded from the Pacific coasts of America.

TYPE MATERIAL. a. LECTOTYPE, a fish of 43.0 mm S.L. *ex* Godeffroy Museum Reg. No. 2152, from Samoa in 1866, NMV.4282.

b. PARALECTOTYPE, a fish of 40.8 mm S.L. (source as above).

There are two further specimens, 49.1–51.5 mm S.L. *ex* Godeffroy Museum, from Samoa in 1869, NMV.4328 (locality correctly stated as Samoa on label).

DESCRIPTION. A fish, 43.0 mm S.L., LECTOTYPE, *ex* Samoa ; in fair condition but dorsal and anal fins slightly damaged and caudal lobes broken, NMV.4283.

Br.St. ?, D ii 8, P i 11, V i 7, A ii 8, g.r. 30.

In percentages of standard length : body depth 18.8, body width 9.1, head length 25.6 ; snout length 7.0, eye diameter 7.4, length of upper jaw 9.3, length of lower jaw 10.7 ; pectoral fin length 12.6, pelvic fin length 10.9, length of anal base 8.1 ; pre-dorsal distance 47.5, pre-pelvic distance 56.5, pre-anal distance 79.5.

Body a little compressed, its width twice in depth, belly rounded and without scutes except for W-shaped pre-pelvic scute ; head longer than body depth ; eye diameter a little greater than snout length. Upper jaw reaching to anterior eye border ; pre-maxillae triangular, toothless ; maxillae toothless ; two supra-maxillae, the 1st (anterior) plate-like and attached to upper edge of maxilla, the 2nd (posterior) supra-maxilla with slender anterior shaft and expanded posterior part, the latter as deep as long (about 1.0 mm), its upper profile rising steeply, its lower profile joining anterior shaft opposite that of upper profile (as in *Sardinella* ; cf. the more asymmetrical shape in *Harengula*). Lower jaw about twice as long as deep, highest point in first third of length ; articulation of lower jaw below vertical from anterior pupil border.

Posterior border of operculum with slight indentation in upper part ; lower border of operculum horizontal. Cleithrum with well developed fleshy cleithral lobes. Isthmus silvery, sterno-hyoideus muscle ending abruptly anteriorly, the urohyal exposed in front of this until concealed by gill membrane. Gillrakers long, slender, about $\frac{1}{2}$ eye diameter, lined with 20–25 fine serrae on each side ; about 6 short gillrakers on posterior face of 3rd epibranchial ; gill filaments about $\frac{2}{3}$ length of gillrakers. Pseudobranch present, exposed, about $\frac{7}{8}$ eye diameter. Dorsal surface of head without striae, posterior frontal fontanelles together almost circular, 0.9 mm long (equal to pupil), anterior extension of supra-occipital slender.

Dorsal fin origin nearer to snout tip than to caudal base by just over 1 eye diameter. Pectoral fin tips fail to reach pelvic base by $2\frac{1}{4}$ eye diameters. Pelvic fin base under 8th branched dorsal ray, nearer to anal origin than to pectoral base by $\frac{2}{3}$ eye diameter. Anal fin origin nearer to caudal base than to pelvic base by $\frac{2}{3}$ eye diameter.

Unexposed portion of scales with one main and 2 (anterior) to 4 (posterior) subsidiary complete vertical striae; exposed portion of scale without crenulations, striae or perforations.

Colour : upper $\frac{1}{4}$ brown, remainder silvery; no silvery lateral stripe.

IDENTIFICATION. The absence of a silver lateral stripe (Whitehead, 1962 : 338) and the shape of the posterior frontal fontanelles and posterior supra-maxilla (Whitehead, 1965 : figs. 2, 3), clearly identify the present specimen as *Spratelloides delicatulus*. The smaller pectoral fins place it in the nominate subspecies (Whitehead, 1962 : 347), which is consistent with its presumed provenance (Samoa).

Fowler (1941 : 565) recognized *Alausa alburnus* as a distinct species, but Bertin (1943) and Schultz & Wellander (1953) correctly placed it in the synonymy of *S. delicatulus*.

Family CLUPEIDAE

HERKLOTSICHTHYS Whitley, 1951

Herklotsichthys Whitley, 1951, *Proc. Roy. zool. Soc. N.S.W.*, 1949-50 : 67 (Type : *Harengula dispilonotus* Bleeker).

A single Steindachner species, *Clupea rechingeri*, is rather doubtfully included in this Indo-Pacific genus.

2. *Clupea rechingeri* Steindachner, 1908 = *?Herklotsichthys punctatus* (Rüppell, 1837)

Clupea punctata Rüppell, 1837, *Neue Wirbelth., Fische* : 78, pl. 21 (2) (Red Sea).

Clupea rechingeri Steindachner, 1908, *Sitzb. K. Akad. Wiss. Wien*, **115** (1) : 1424 (Upolu, Samoa).

TYPE MATERIAL. The two specimens described by Steindachner (no size given) cannot now be found.

IDENTIFICATION. The criteria now used to distinguish the genera *Sardinella* and *Herklotsichthys* (Whitehead, 1964a) do not appear in the description of *C. rechingeri* and Steindachner gave no clue to its relationship to other species. Regan (1917 : 392) and Fowler (1941 : 597) identified *Clupea rechingeri* with *Harengula vittata* (= *Sardinella melanura* (Cuvier) *vide* Whitehead, 1967a : 66). The latter has very distinctive black caudal tips (retained in alcohol specimens), whereas Steindachner's description seems to allude to the general darkening of the whole caudal margin found in many species of *Herklotsichthys* and *Sardinella* : *Die Spitzen der Schwanzflossen lappen und der Innenrand derselben sind dunkel angeflogen*. *Herklotsichthys punctatus* is one of the commonest Indo-Pacific clupeids and Steindachner's description fits the species.

SARDINELLA Valenciennes, 1847

Sardinella Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 261 (Type : *Sardinella aurita* Valenciennes).

As yet, there is no modern world-wide study of the *Sardinella* species with 9 pelvic finrays (*S. aurita*, *S. longiceps*, *S. anchovia*, *S. brasiliensis*). In the Indo-Pacific region, *S. aurita* and *S. longiceps* (whose ranges apparently do not overlap) can be easily distinguished (Chan, 1965), but studies of *aurita*-like fishes in the Atlantic have not compared Eastern with Western Atlantic forms, or both with the Western Pacific *S. aurita*, at least on the basis of adequate material.

3. ***Clupea brasiliensis*** Steindachner, 1879
 = ***Sardinella brasiliensis*** (Steindachner, 1879)

Clupea brasiliensis Steindachner, 1879, *Sitzb. K. Akad. Wiss. Wien*, **80** : 182 (fish market, Rio de Janeiro) (*non Clupea brasiliensis* Schneider, 1801 = *Albula vulpes*—the Schneider name now a *nomen oblitum*) ; Idem, 1880, *Ichthyol. Beitr.*, **8** : 64.

Clupea janeiro Eigenmann & Bray, 1894, *Ann. N.Y. Acad. nat. Sci.* : 626 (replacement name for the preoccupied *Clupea brasiliensis* Steindachner).

SYNONYMY. *Clupea brasiliensis* Steindachner (a species of *Sardinella*) is a primary homonym of *Clupea brasiliensis* Schneider (= *Albula vulpes*—Whitehead, 1969b). Fowler (1941 : 602) avoided the issue by resurrecting the earlier Rafinesque name *allecia* for the *Sardinella* species, but this name is both doubtfully legal (Whitehead, 1967a : 40) and applies to the Mediterranean species of *Sardinella* ; as shown below, Steindachner's Brazilian species is possibly distinct. Myers (in Rivas, 1964 : 410) believed that a new name was required for the latter, but overlooked *Clupea janeiro* of Eigenmann and Bray. The Schneider name has not been used, however, as a senior synonym for over fifty years (see full synonymies in Fowler, 1941 and Hildebrand, 1964) and it thus qualifies as a *nomen oblitum* under Article 23(b) of the International Code. Application will be made to place the Schneider name on the Official Index and thus to release the Steindachner name for this species of *Sardinella*.

TYPE MATERIAL

- a. LECTOTYPE, a fish of 143.3 mm S.L., *ex* Rio de Janeiro in 1877, NMV.1156 (jar labelled VII 126 n.sp.).
- b. PARALECTOTYPES, 2 fishes, 121.0–121.2 mm S.L., *ex* Rio de Janeiro in 1874, NMV.1158 (jar labelled I 13 . . .).
- c. PARALECTOTYPES, 2 fishes, 114.4–140.7 mm S.L., *ex* Rio de Janeiro in 1874, NMV.1159 (jar labelled I 1356 pt.b).
- d. PARALECTOTYPES, 4 fishes, 116.7–120.7 mm S.L., *ex* Rio de Janeiro in 1874, NMV.1160 (jar labelled I 1216a).
- e. PARALECTOTYPE, 1 fish, 120.5 mm S.L., *ex* Rio de Janeiro, in 1874, NMV.1161 (jar labelled I 1623).
- f. PARALECTOTYPES, 4 fishes, 114.0–121.7 mm S.L., *ex* Rio de Janeiro in 1874, NMV.1162 (jar labelled I 1216 pt.).

g. ? **PARALECTOTYPE**, 1 fish, 148.3 mm S.L., *ex* Rio de Janeiro in 1879, NMV. 1155 (jar labelled coll. Pape 62). This fish may not have been available when the original description was made.

DESCRIPTION. A fish, 143.3 mm S.L., 180 mm tot.l. (estimated, caudal tips damaged), **LECTOTYPE**, *ex* Rio de Janeiro fish market in 1874, in good condition except caudal, NMV.1156.

Br.St. 6, D v 14, P i 15, V i 8, A iii 15, g.r. 155, scutes 19+14.

In percentages of standard length : body depth 22.5, body width 12.4, head length 27.7 ; snout length 7.5, eye diameter 6.6, length of upper jaw 11.0, length of lower jaw 13.9, height of lower jaw 6.0, sub-ocular depth 7.3, least post-orbital distance 11.9 ; pectoral fin length 16.9, pelvic fin length 9.7, length of anal base 12.8 ; predorsal distance 45.5, pre-pelvic distance 52.7, pre-anal distance 79.2.

Body a little compressed, its width $1\frac{1}{2}$ in depth, belly rounded before pelvic base but scutes more keeled behind ; head length greater than body depth, post-orbital portion a little less than $\frac{1}{2}$ length of head. Snout a little longer than eye diameter. Upper jaw toothless, reaching to vertical from eye centre ; two supra-maxillae, the posterior with slender anterior shaft and lozenge-shaped expanded portion posteriorly, its upper and lower profiles meeting anterior shaft at the same point. Lower jaw toothless, rising steeply anteriorly, its height $2\frac{1}{2}$ times in its length, its articulation slightly behind vertical from eye centre. Fine granular teeth present on tongue, palatines and ectopterygoids.

Posterior border of operculum with slight indentation in its upper part, lower border horizontal ; sub-operculum rectangular but posterior angle evenly rounded ; inter-operculum about $\frac{1}{3}$ eye diameter at widest point. Posterior border of gill opening with two fleshy lobes ; cleithral lobe present ; isthmus slender, tapering, the sterno-hyoideus muscle extending forward to gill membrane. Gillrakers fine and slender, the longest 8.9 mm (a little more than eye diameter) ; mediopharyngobranchial present, its length $\frac{2}{3}$ eye diameter, bearing the first thirty upper gillrakers ; over one hundred slender gillrakers present on posterior face of 3rd epibranchial ; gill filaments of anterior hemibranch on first arch $\frac{1}{2}$ eye diameter and $\frac{3}{4}$ length of those of posterior hemibranch. Pseudobranch present, exposed, extending onto inner face of operculum, equal to eye diameter, with 20 filaments ; ventral border forming a distinct ridge with a longitudinal groove below for reception of tips of hypobranchial rakers of first arch. Fronto-parietal region of head with two cuneiform areas bearing about ten longitudinal striae, a well-defined transverse ridge on the supra-occipital and several smaller striae above the eyes.

Dorsal fin origin nearer to snout tip than to caudal base by $1\frac{2}{3}$ eye diameters ; base of fin invested in low scaly sheath. Pectoral fin tips fail to reach pelvic base by $1\frac{1}{3}$ eye diameters ; no axillary scale but a groove above first unbranched ray for reception of fin. Pelvic fin base nearer to pectoral base than to anal origin ; axillary scale present, $\frac{3}{4}$ length of fin. Anal fin origin nearer to caudal base than to pelvic base by $\frac{1}{2}$ eye diameter ; base of fin invested in low scaly sheath, final anal ray much branched and about twice length of antepenultimate ray.

Unexposed portion of scales with one continuous and 2 (anterior) to 4 (posterior)

minor vertical striae, the later broken in centre of scale (except for posterior striation in some post-dorsal scales) ; exposed border of scale with fine crenulations and faint horizontal lines.

Colour : upper $\frac{1}{4}$ of body brown, remainder silvery ; small dark semicircular area on posterior border of operculum due to absence of guanine layer on inner face ; faint dark tips to dorsal branched rays.

IDENTIFICATION. Regan (1917 : 378) placed *Clupea brasiliensis* Steindachner in the synonymy of the widespread *Sardinella aurita* Valenciennes, but Longley & Hildebrand (1941) noticed higher gillraker counts in three out of four syntypes of *Sardinella anchovia* Valenciennes (= *S. aurita*) and recognized these three specimens as distinct and most likely Steindachner's *brasiliensis*. Hildebrand (1964 : 399) separated *S. brasiliensis* from the two other Western Atlantic species, chiefly on the basis of its higher gillraker count (numbers increase in larger fishes, however), which he cited as :

<i>S. brasiliensis</i>	110-130 (160-178 in Longley & Hildebrand, 1941)
<i>S. pinnula</i> Bean	75-80
<i>S. anchovia</i>	55-100

The three doubtful syntypes of *S. anchovia* (104.5-143.6 mm S.L.) have been re-examined (Whitehead, 1967a : 42) and their high gillraker count was confirmed (151, 174, 179). Another difference between these *brasiliensis*-like syntypes and the remaining true lectotype of *S. anchovia* was found to be the greater depth of the cheek in the former (greater than vertical eye diameter). On the basis of gillraker counts and cheek depth it was accepted that *S. brasiliensis* differed from other Western Atlantic species and probably also from *S. aurita* of the Mediterranean, Eastern Atlantic and Pacific (which is also most likely one of the Western Atlantic species, i.e. the *S. anchovia* of authors—see Whitehead, 1967a : 43).

Examination of specimens of *S. aurita* from the Mediterranean, West Africa and the Philippines has now shown, however, that *S. brasiliensis* cannot be separated from them on its apparently deeper cheek. Furthermore, the total range in gillraker numbers (66-166 *vide* Chan, 1965 ; up to 280 in 350 mm fishes *vide* Rossignol, 1955) means that separation will depend on a formula relating gillraker counts to length of fish. Lima (1966) described as *S. brasiliensis* six specimens of 128-160 mm S.L. from Estado do Ceará, Brazil. Her gillraker counts of 64-128, however, appear to be too low for fishes of this size, at least as far as the figures for the types of *brasiliensis* are concerned ; on the other hand, they are close to the numbers cited by Hildebrand (1964). The identity of *S. brasiliensis* must depend, therefore, on examination of large samples, especially from the Western Atlantic. Descriptions of the types of *brasiliensis*, *anchovia* and *aurita* reveal only small differences which, although not totally vindicating Regan's synonymizing of the three, at least suggest that no Western Atlantic study can afford to ignore the Eastern Atlantic, Mediterranean and Pacific forms of *S. aurita*.

ESCUALOSA Whitley, 1940

Escualosa Whitley, 1940, *Aust. Zool.*, **9** (4) : 402 (Type : *Clupea macrolepis* Steindachner = *Kowala thoracata* Valenciennes).

Generic and species synonymies are discussed in Whitehead (1964a ; 1967a : 70) and Whitehead *et al.* (1966 : 70) and a key to this section of the Clupeinae appears in Whitehead (1968).

4. ***Clupea macrolepis*** Steindachner, 1879
= ***Escualosa thoracata*** (Valenciennes, 1847)

Kowala thoracata Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 363 (Pondicherry ; type redescribed in Whitehead, 1967a).

Clupea macrolepis Steindachner, 1879, *Denkschr. Akad. Wiss. Wien*, **41** (2) : 13 (Townsville, Queensland ; type of *Escualosa* Whitley, 1940).

TYPE MATERIAL. HOLOTYPE, a fish of 64 mm S.L., *ex* Townsville, Cleveland Bay, Queensland, Australia, coll. Baron Ferdinand von Müller, SMNS.2292.

DESCRIPTION. Proportional and meristic characters for the holotype were given in Whitehead (1964a : 44, Table III). In all respects the type conforms to the more detailed description of the species given in the same publication (p. 45) and in Whitehead (1967a : 71).

SYNONYMY. *Clupea macrolepis* Steindachner has been shown to be a junior synonym of *Kowala thoracata* Valenciennes (Whitehead, 1964a : 43). Whitley (1940 : 402) designated *Clupea macrolepis* type of *Escualosa* Whitley. Since *Leptogaster* Bleeker proved to be a *nomen oblitum* (Whitehead *et alii*, 1966 : 70) and *Kowala* Valenciennes a synonym of *Sardinella* (Whitehead, 1964a : 52), the genus *Escualosa* was recognized, containing the single species *E. thoracata*. Whitley (1940 : fig. 9) figured a specimen of *Harengula* sp. and suggested that it represented the adult of his *Escualosa macrolepis*. The following year (Whitley, 1941 : 1) he found in Paris a replacement specimen of the type of *Harengula abbreviata* Valenciennes (the real type being missing), identifying it as *Kowala castelnaui* Ogilby "whose name is obviously a synonym of *abbreviata* which belongs to my genus *Escualosa*, 1940". In fact, the replacement specimen does not match the description of *abbreviata* and the latter name should be considered a *nomen dubium* (Whitehead, 1967a : 69). Whitley's specimen of *Harengula* appears to be *Herklotsichthys castelnaui* and *Escualosa* remains a monotypic genus distinguished by possession of 7 pelvic rays, a silver lateral stripe and a large rectangular 2nd supra-maxilla (see key, Whitehead, 1968 : 478).

RHINOSARDINIA Eigenmann, 1912

Heringia Fowler, 1911, *Proc. Acad. nat. Sci. Philad.*, **63** : 207 (Type : *Clupea amazonica* Steindachner) (name preoccupied in Diptera—Myers, 1929, *Copeia* : 1).

Rhinosardinia Eigenmann, 1912, *Mem. Carnegie Mus.*, **5** : 445 (Type : *Rhinosardinia serrata* Eigenmann = *R. amazonica* Steindachner).

The curious retrorse spine at the anterior end of the maxilla sets this genus apart from all others (see key in Whitehead, 1968 : 478). A small projection occurs in

Escualosa (Whitehead, 1964a : fig. 2c) but this is blunt and points upwards and not backwards. In other respects *Rhinosardinia* is very similar to the South American genera *Lile* and *Ramnogaster*. Regan (1917 : 394) placed *Rhinosardinia* (as *Heringia*) with *Lile*, *Sardinella* and *Harengula*, i.e. in the Clupeinae. Hildebrand (1964 : 261) allied *Rhinosardinia* with the Pristigasterinae, but current definitions of the clupeid subfamilies (e.g. Whitehead *et alii*, 1966 : 37), although by no means satisfactory, exclude *Rhinosardinia* from the Pristigasterinae, because of its short anal fin (under 20 rays ; cf. over 30), and place it in the Clupeinae.

At species level, the South American clupeids show rather little relationship to the West African or Indo-Pacific clupeids (only *Sardinella aurita* is found on both sides of the Atlantic), and only the genera *Sardinella*, *Ilisha* and *Pellona* are shared (the last not from West Africa). It has been argued, therefore (Whitehead, 1968), that the South American Clupeinae have evolved in isolation. The similarities between *Rhinosardinia* and the Indo-Pacific *Escualosa* may thus be coincidental, resulting from relatively limited variations possible within the clupeine framework.

In *Escualosa*, as also in *Rhinosardinia* (but less so in *R. bahiensis*) the upper jaw is more or less notched, a condition typical of the shads (subfamily Alosinae). Although *Brevoortia*, *Ethmidium*, *Ethmalosa* and the Indo-Pacific shads (*Hilsa*, *Gudusia*) have very long and numerous gillrakers and no jaw teeth, teeth and short, sparse rakers are found in some species of *Alosa* (*sensu* Svetovidov, 1964, i.e. including *Pomolobus* and *Caspialosa*). Future work may show that *Rhinosardinia* can be derived as convincingly from the *Alosa* stem as from the Western Atlantic Clupeinae.

**5. *Clupea amazonica* Steindachner, 1879
= *Rhinosardinia amazonica* (Steindachner, 1879)**

Clupea amazonica Steindachner, 1879, Sitzb. K. Akad. Wiss. Wien, **80** : 183 (Amazon R. at Pará ; 4 fishes, 40–75 mm tot. l.) ; *Idem*, 1880, Ichthyol. Beitr., No. 8 : 65 (repeat).
Rhinosardinia serrata Eigenmann, 1912, Mem. Carnegie Mus., **5** : 445, text fig. 39, pl. 62 (figs. 3 and 4) (*ex* Morawhanna and Mora Passage, British Guiana).

TYPE MATERIAL. a. LECTOTYPE, a fish of 54.8 mm S.L. (74.0 mm tot.l.), *ex* Pará, Amazon River in 1879, NMV.1104.

b. PARALECTOTYPES, 3 fishes 31.2–42.2 mm S.L. from the same jar.

Steindachner listed only 4 fishes. A fifth specimen in this jar (25.9 mm S.L., 32 mm tot.l.) is too small to have been part of the original description.

DESCRIPTION. A fish 54.8 mm S.L. (74.0 mm tot.l.) *ex* Pará, Amazon River, in good condition, NMV.1104.

Br.St. 5 (left 6), D ii 13, P i 11, V i 7 (both sides), A iii 13, g.r. 38, scutes 17+11.

In percentages of standard length : body depth 30.3, head length 24.1 ; snout length 5.75, eye diameter 7.3, length of upper jaw 9.85, length of lower jaw 9.5, depth of lower jaw 5.6 ; pectoral fin length 19.8, pelvic fin length 12.4, length of anal fin base 13.0, length of dorsal base 14.2, height of dorsal fin 18.6 ; pre-dorsal distance 51.0, pre-pelvic distance 51.0, pre-anal distance 76.5 ; depth of caudal peduncle 13.3.

Body compressed, belly with trenchant keel of scutes, body depth greater than head length. Snout shorter than eye diameter. Upper jaw with two supra-maxillae,

the 1st (anterior) slender, the 2nd (posterior) with diamond shaped expanded portion reaching to posterior tip of maxilla ; minute teeth present on lower edge of maxilla below centre of 2nd supra-maxilla, and a sharp retrorse spine (= to half pupil diameter) on upper edge of maxilla in front of anterior supra-maxilla ; upper jaw with a slight median notch. Lower jaw profile rising steeply, its deepest part in first $\frac{1}{3}$ of its length, the jaw 1.6 times as long as deep. No teeth on pre-maxillae or lower jaw or within mouth.

Gillrakers fine and slender, $\frac{1}{2}$ eye diameter and a little longer than corresponding gill filaments ; about 10 short rakers on posterior face of 3rd epibranchial. Pseudo-branch $\frac{3}{4}$ eye diameter, with 11 filaments. Operculum with anterior and posterior margins parallel, the lower border rising at about 40° ; sub-operculum rectangular with rounded posterior border ; inter-operculum deep posteriorly, tapering evenly to the lower jaw articulation. Fronto-parietal region of head smooth, posterior frontal fontanelles occluded.

Dorsal fin origin midway between tip of snout and base of caudal fin ; dorsal height (last unbranched ray) 1.30 times length of dorsal base. Pectoral fin failing to reach pelvic base by just over 1 eye diameter ; no axillary scale present. Pelvic fin base in advance of dorsal origin by almost 1 pupil diameter and equidistant between pectoral base and anal origin ; axillary scale present, $\frac{1}{3}$ length of fin. Anal origin equidistant between pelvic base and base of caudal fin. Depth of caudal peduncle 2.27 times in body depth.

Unexposed portion of scales with one continuous vertical striation and up to three small radiating striae not reaching to centre of scale ; exposed portion of scale with two horizontal striae converging to centre of scale. Small scales present on caudal.

Colour : overall brownish, but with no suggestion of a silver lateral stripe (absent also in paralectotypes).

SYNONYMY. Regan (1917 : 394) considered *R. serrata* Eigenmann a synonym of *R. amazonica*, but Hildebrand (1964 : 415) after " careful rereading of the original description of *amazonica* " decided to separate the two on small differences in body

	<i>R. amazonica</i> (LECTOTYPE) NMV.1104	<i>R. serrata</i> (SYNTYPE) USNM.66284	<i>R. serrata</i> (4 SYNTYPES) BMNH.1911.10.
			31.452-5
S.L.	54.8	47.3	44.5-49.6
As % of S.L.			
Body depth	30.3	30.0	28.5-30.5
Head length	24.1	23.8	21.6-23.3
Caudal peduncle depth	13.3	13.1	12.7-13.5
Dorsal fin :			
base	14.2	12.7	12.2-13.8
height	18.6	18.0	18.7-20.0
height			
base	1.31	1.42	1.43-1.49
Body depth			
Caudal ped. l.	2.27	2.29	2.18-2.31
Gillrakers	38	35	33, 34, 34, 35

depth, depth of caudal peduncle, head and snout length and length of dorsal fin base. A comparison between five syntypes of *R. serrata* and the lectotype of *R. amazonica* does not bear out Hildebrand's distinction between these two nominal species.

The slightly longer dorsal fin base in the lectotype of *R. amazonica* and its slightly higher gillraker count hardly justify separation of the two species. The range of *R. amazonica* thus extends from the mouth of the Amazon, through the Guianas to the San Juan river in Venezuela.

6. *Pellonula bahiensis* Steindachner, 1879
= *Rhinosardinia bahiensis* (Steindachner, 1879)
 (Plate 1b)

Pellonula bahiensis Steindachner, 1879, *Sitzb. K. Akad. Wiss. Wien*, **80** : 181, pl. 3 (fig. 2) (*ex* Bahia, 8 fishes to 100 mm tot.l.) ; *Idem*, 1880, *Ichthyol. Beitr.*, No. 8 : 63, pl. 3 (fig. 2) (repeat).

TYPE MATERIAL. LECTOTYPE, a fish of 69.1 mm S.L. (90.5 mm tot.l.), in good condition but some scales missing, *ex* Bahia in 1879, NMV.2870.

PARALECTOTYPE, a fish of 70.5 mm S.L. from the same bottle.

DESCRIPTION. A fish, 69.1 mm S.L. (90.5 mm tot.l.), LECTOTYPE, *ex* Bahia, NMV.2870.

Br.St. 6 (6 right), D iii 15, P i 13, V i 7, A iii 14, g.r. 32, scutes 17+11.

In percentages of standard length : body depth 27.3, body width 11.1, head length 25.0 ; snout length 6.4, eye diameter 8.7, length of upper jaw 11.9, length of lower jaw 11.9, depth of lower jaw 6.2 ; pectoral fin length 15.9 pelvic fin length 12.7, length of dorsal fin base 17.5, height of dorsal fin 19.0, length of anal fin base 16.2 ; pre-dorsal distance 46.1, pre-pelvic distance 49.8, pre-anal distance 72.5.

Body compressed, its width $2\frac{1}{2}$ times in its depth, belly keeled, scutes with long sharp spines partly concealed by scales on either side of midline ; head a little shorter than body depth. Snout a little shorter than eye diameter. Upper jaw reaching almost to vertical from eye centre ; two supra-maxillae, the 1st (anterior) long and plate-like, the 2nd (posterior) of typical *Harengula* shape and reaching to posterior tip of jaw ; maxilla with a small blunt projection (? damaged ; = retrorse spine in paralectotype) on upper face of maxilla in front of 1st supra-maxilla ; minute denticulations along lower edge of maxilla below 2nd supra-maxilla ; upper jaw without marked notch. Lower jaw profile rising steeply, its deepest part in first $\frac{1}{3}$ of its length, the jaw 1.91 times as long as deep. Small conical teeth present at dentary symphysis (left 4, right 3), on pre-maxillae (left 4, right 7) and even smaller on palatines and ecto-pterygoids.

Gillrakers fine and slender, the longest just under half eye diameter, $1\frac{1}{4}$ times length of corresponding gill filaments ; seven short triangular rakers present on posterior face of third epibranchial ; short mediopharyngobranchial present, bearing 6 gillrakers. Pseudobranch present, exposed, $\frac{3}{4}$ eye diameter, with 14-15 filaments. Cleithral lobe present. Exposed portion of inter-operculum a narrow crescent, less than half depth of sub-operculum. Frontals diverging in the midline posteriorly to expose a triangle of the supra-occipital ; posterior frontal fontanelles not exposed ;

fronto-parietal region with a series of short longitudinal striae (not as strongly developed, however, as in e.g. *Sardinella*).

Dorsal fin origin nearer to snout than to caudal by just over 1 eye diameter and in advance of vertical from pelvic base by 1 pupil diameter ; base of fin 1.09 times in its height. Pectoral fin tips failing to reach pelvic base by just over 1 eye diameter ; axillary scale absent (apparently) but a short groove present above proximal $\frac{1}{3}$ of first ray. Pelvic fin base nearer to pectoral base than to anal origin by $\frac{1}{2}$ pupil diameter ; axillary scale present, a little over $\frac{1}{2}$ length of fin. Anal fin origin about equidistant between pelvic and caudal bases ; a low sheath of scales along base of fin.

Scales : unexposed portion of scale with one major and up to three minor striae, the former vertical and continuous across scale, the latter radial and only occasionally traversing scale ; exposed portion of scale without striae or with one or two very short radial striae.

Colour : body brown, with very distinct silver lateral band from opercular opening to caudal base, almost as broad as eye ; opercular series and belly silvery.

NOTE. Regan (1917 : 395) doubted that *Pellonula bahiensis* could be separated from *Clupea amazonica* on the basis of its silver lateral stripe, since specimens of the latter " also show a faint lateral band in certain lights. " The stripe in *R. bahiensis* is, however, quite as distinct as that which separates e.g. *Spratelloides gracilis* from *S. delicatulus* in all except post-larval size groups. It was well illustrated by Steindachner (see Plate 1b).

Rhinosardinia amazonica and *R. bahiensis* were clearly distinguished by Hildebrand (1964 : 411), but examination of the types necessitates some modifications to the key (as stated earlier, *R. serrata* is a synonym of *R. amazonica*).

KEY TO SPECIES *Rhinosardinia*

- 1 Silver lateral stripe present ; exposed portion of scales without 2 prominent horizontal striae ; dorsal fin origin nearer to snout than to caudal base by 1 eye diameter ; inter-operculum visible as narrow crescent, $\frac{1}{2}$ as deep as sub-operculum *Rhinosardinia bahiensis* (Steind.)
- 2 No silver lateral stripe ; exposed portion of scales with 2 prominent horizontal striae ; dorsal fin origin equidistant between snout tip and caudal base ; inter-operculum broadly exposed, at its widest as deep as sub-operculum *Rhinosardinia amazonica* (Steind.)

SARDINOPS Hubbs, 1929

Sardinops Hubbs, 1929, *Proc. Calif. Acad. Sci.*, **18** (11) : 264 (Type : *Meletta caerulea* Girard).

As in other wide-ranging genera with a discontinuous distribution, the various forms of *Sardinops* have sometimes been considered to be distinct species and sometimes merely subspecies. Regan (1916 : 14) and Chabanaud (1926) suspected the latter but excluded *S. neopilchardus* of Australia and New Zealand ; Svetovidov (1952 : 177) recognized five subspecies of *Sardinops sagax*, but with some reservation regarding *neopilchardus*, in which the head is longer, the maxilla shorter and the gillrakers less numerous than in the other forms. On present evidence, Svetovidov's solution seems best.

7. *Alausa fimbriata* Kner & Steindachner, 1866
 = *Sardinops sagax sagax* (Jenyns, 1842)
 (Plate 1c)

Clupea sagax Jenyns, 1842, *Zool. Beagle, Fish.* : 134 (ex San Lorenzo I., Lima).

Alausa fimbriata Kner & Steindachner, 1866, *Sitzb. K. Akad. Wiss. Wien*, 54 : 386, pl. 15 ("Valparaiso?", no size, from Museum Godeffroy).

LOCALITY. As noted earlier (p. 6), Steindachner confused the reference number and locality of this species with that of his *Alausa alburnus*. The correct locality is thus Valparaiso, Chile.

TYPE MATERIAL. Intensive search produced no specimen labelled *Alausa fimbriata* in Vienna. But Steindachner's description and figure are quite sufficient to identify this species and provision of a neotype would serve no useful purpose.

IDENTIFICATION. Steindachner's pl. 15 (shown here, Plate 1c) shows the striations on the operculum, the enlarged anal rays and the large alar scales that characterize members of *Sardinops*; the description is quite consistent with this identification. A series of black spots often occurs along the flank but this was apparently not the case in Steindachner's specimen.

Steindachner appears to have been unaware of Jenyns work on the *Beagle* collection.

8. *Clupea neopilchardus* Steindachner, 1879
 = *Sardinops sagax neopilchardus* (Steindachner, 1879)

Clupea lata Richardson, 1843, *Trav. N.Z.* (Dieffenbach), 2 : 221 (on Solander MS. name *Clupea lata*—*nomen nudum*).

Clupea neopilchardus Steindachner, 1879, *Denkschr. Akad. Wiss. Wien*, 41 : 12 (not quite 170 mm, ex Hobson's Bay, Victoria, type in Stuttgart Museum).

TYPE MATERIAL. The type is apparently no longer present in Stuttgart. This sub-species is sufficiently well defined geographically (southern Australia and New Zealand—nearest related forms in South Africa and along Pacific coast of South America) for the provision of a neotype to be unnecessary at the present time, particularly in view of the excellent study of the Australian form by Blackburn (1949).

Richardson's *Clupea lata* is not accompanied by any description but merely a reference to Solander's MS. description in his notebook (*Pisces Australiae*, p. 17) made during Captain Cook's first voyage to the Pacific. Solander's description reads :

Clupea lata B.18

Habitat Tolaga

Argentea, nitidipinna ; Dorso e cinereo caeruleo nitente, ut et superna pars capitis.

Pinna analis basi plumbea, alias omnes colore corporis ubi sita.

Pinna caudalis tota plumbea

Iris argentea, superne semper nebula nigra.

This description is not adequate to identify the species and no drawing of *Clupea lata* was made by Sydney Parkinson, the artist on this voyage. The name *Clupea lata* is a *nomen nudum*.

9. *Clupea setosa* Steindachner, 1869
= *Ethmalosa fimbriata* (Bowdich, 1825)
(Plate 2a)

Clupea fimbriata Bowdich, 1825, *Excurs. Madeira* : 234, fig. 44 (Porto Praya, Cape Verde Is.—probably the Gambia *vide* Whitehead, 1967b : 590).

Clupea setosa Steindachner, 1869, *Sitzb. K. Akad. Wiss. Wien*, **60** : 311, pl. 6 (*ex* Mazatlan stated—in fact West Africa) ; *Idem*, 1869, *Ichthyol. Notizen*, No. 9 : 22, pl. 6 (repeat).

LOCALITY. Steindachner (1882 : 14) subsequently realized that his specimens had not come from Mazatlan (Mexico) but were from the coasts of Liberia and Gabon, West Africa.

TYPE MATERIAL. LECTOTYPE, a fish of 184.0 mm S.L. (253.0 mm tot.l.), *ex* West Africa (Liberia or Gabon coasts), NMV.4173.

PARALECTOTYPES, two fishes, 174.5–178.0 mm S.L., as above, caudal lobes damaged.

The specimens are accompanied by labels reading :

“ *Coll. Musei Vindobonensis* 4173

CLUPEA altata Std. ALTATA Steind. 1878 I 20 ”

and

“ *Coll. Musei Vindobonensis* 4173

CLUPEA setosa Steind. ALTATA (Mexico Sinaloa) 1878 ”.

DESCRIPTION. A fish, 184.0 mm S.L. (253.0 mm tot.l.), LECTOTYPE, *ex* West Coast of Africa, in good condition. NMV.4173

Br.St. 6, D iv 14, P i 14, V i 7, A iii 18, g.r. 130, scutes 18+12.

In percentages of standard length : body depth 39.4, body width 13.4, head length 34.0 ; snout length 8.3, eye diameter 7.5 ; upper jaw length 15.5, lower jaw length 18.0, post-orbital distance 18.7 ; pectoral fin length 21.8, pelvic fin length 12.7, length of anal fin base 17.9 ; pre-dorsal distance 49.2, pre-pelvic distance 56.2, pre-anal distance 76.5.

Body compressed, its width 3 times in its depth, the latter a little greater than head length ; belly keeled, but scutes lying in narrow groove formed by scales and thus scarcely projecting below profile of body. Head with adipose tissue covering much of upper part, adipose eyelid present and covering all but a third of eye. Cutaneous sensory canals on operculum, pre-operculum and 2nd sub-orbital and continued on scales behind occiput and around upper border of gill opening.

Snout a little longer than eye. Upper jaw with distinct median notch into which distal tip of lower jaw fits. Maxilla without longitudinal ridges, reaching posteriorly to vertical from just behind eye centre ; two supra-maxillae. No teeth in jaws or on tongue. Operculum with lower border rising steeply upwards ; anterior border of operculum with slight cut-away, exposing junction of sub- and inter-opercula.

Pseudobranch present, exposed, a little greater than snout length, the lower border forming a distinct ridge with a groove below it. Gillrakers as described in the neotype of *Clupea fimbriata* Bowdich (see Whitehead, 1967b : 591) ; longest rakers on lower arm of first arch equal to eye diameter and about three times length of corresponding filaments.

Dorsal fin origin nearer to snout than to caudal base by $\frac{3}{4}$ eye diameter ; first unbranched ray very small. Pectoral fin tip almost reaching to pelvic base ; one large and two small scales in axil of fin, forming a groove along $\frac{1}{2}$ length of fin. Pelvic fin base nearer to pectoral base than to anal origin by $\frac{1}{4}$ eye diameter. Anal fin origin nearer to pelvic base than to caudal base by $\frac{1}{2}$ eye diameter.

Scales adherent, about 40 in lateral series ; posterior edges fimbriated, as in Steindachner's figure (see Plate 2a).

Colour : uniform brown with dark brown at tips of anterior dorsal rays.

IDENTIFICATION. The genus *Ethmalosa* is monotypic and occurs only off the West Coast of Africa. The synonymy of the species is fully dealt with by Whitehead (1967b). The relationship of *Ethmalosa* to other genera of shads is discussed by Whitehead (1965b : 153).

10. *Clupea notacanthoides* Steindachner, 1869
= *Ethmidium maculatum notacanthoides* (Steindachner, 1869)
 (Plate 2 b)

Alausa maculata Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 430 (Valparaiso—holotype redescribed by Whitehead, 1967a : 88).

Clupea notacanthoides Steindachner, 1869, *Sitzb. K. Akad. Wiss. Wien*, **60** : 309, pl. 7 (Mazatlan stated—probably erroneous) ; *Idem*, 1869, *Ichthyol. Notizen*, No. 9 : 20, pl. 7 (repeat).

Ethmidium chilcae Hildebrand, 1946, *Bull. U.S. natl. Mus.*, No. 189 : 82 (Callao and Chilka Bay, Peru).

LOCALITY. No mention of Steindachner's species is made by Jordan (1895) in his list of fishes from Sinaloa, nor in the check-list of Jordan, Evermann & Clark (1930). In view of the mislabelling of the ' Mazatlan ' specimens of *Clupea setosa* (see p. 17), it seems probable that Steindachner's *Clupea notacanthoides* came from the normal range of *Ethmidium maculatum*, i.e. Peru or Chile.

TYPE MATERIAL. Intensive search in Vienna has failed to produce the specimen(s) on which the description was made ; no size is stated, but the figure suggests a fish of about 175 mm S.L. (see Plate 2b).

DESCRIPTION. (based on Steindachner's description).

Br.St. 9, D 20, P 17, V 7, A 14, scales in lateral series *ca* 50, 7 predorsal scutes (? error for 17), ventral scutes *ca* 18+17.

In percentages of standard length : body depth 30, head length 32.

In percentages of head length : snout length 21, eye diameter 15.8, interorbital 25, lower jaw 55.5 ; longest dorsal ray 44.5, pectoral length 36.5 (57 in figure).

Dorsal origin $1\frac{1}{2}$ eye diameters nearer to snout than to caudal base. Pectoral falling short of pelvic base by just over 1 eye diameter (according to figure) ; a series

of enlarged scales above first ray. Pelvic base equidistant between tip of snout and caudal base. Anal base about one eye diameter shorter than head length; longest ray $1\frac{1}{4}$ eye diameters.

Colour : a series of six black spots on the flank below the midlateral line.

IDENTIFICATION. The well illustrated dorsal scutes and high branchiostegal count confirm that Steindachner's specimen was a species of *Ethmidium*. Hildebrand (1946 : 84-85) proposed a new species, *Ethmidium chilcae*, for his Peruvian specimens, which he distinguished from *E. maculatum* of Chile in the following way.

	<i>E. maculatum</i> Lota, Chile (70-113 mm S.L.)	<i>E. chilcae</i> Callao & Chilka Bay, Peru (ca 100-212 mm S.L.)
Head in S.L.	3.25-3.4 (29.4-30.8%)	3.0-3.1 (32.3-33.3%)
Depth in S.L.	2.75-2.9 (34.5-36.4%)	2.8-3.1 (32.3-35.7%)
Caudal peduncle depth in head length	2.80-2.95	3.20-3.75
Pectoral fin tip short of pelvic base	by eye diam.	by pupil diam. or "less than eye" in adults
Ventral profile	more convex	
Scales	nearly smooth	denticulate

Examination of larger specimens from Chile (over 200 mm S.L.) shows that in adults the convexity of the belly profile, the denticulations on the posterior edge of the scale and the depth of the body reach the condition specified by Hildebrand for his Peruvian *E. chilcae* (e.g. in the type of *E. maculatum* from Valparaíso as redescribed in Whitehead, 1967a and in two British Museum specimens from the Gulf of Arauco, Chile). The only Peruvian specimen in the British Museum collection is a large adult, 245 mm S.L., which agrees with Hildebrand's diagnosis of *E. chilcae* in having a large head (35.8% of S.L.), a caudal peduncle depth 3.65 times in head length and denticulate scales. Unfortunately, the belly and pelvic fins are missing. Eight Peruvian specimens in the Copenhagen collections (*ex* Callao, 180-266 mm S.L., ZMC. 544-5 and 18289-91) agree with Hildebrand's diagnosis in head length (31.1-33.0% of S.L.), body depth (32.7-36.2% of S.L.), caudal peduncle depth in head length (3.07-3.75 times) and distance between pectoral tip and pelvic base ($1\frac{1}{4}$ - $2\frac{1}{4}$ pupil diameters, but less than eye). The scales bear 20-22 denticulations on the posterior margin.

On the basis of the material examined and the small size of Hildebrand's Chilean specimens, it is likely that head length may distinguish Peruvian from Chilean stocks, but that body depth, scale form and apparent pectoral length are probably dependent on the size of the fish or on exogenous factors (trophic conditions).

Mann (1954) regarded Hildebrand's Peruvian material as a subspecies of *E. maculatum* and stated that it reached as far south as Antofagasta in Chile, its place then being taken by the nominate form. Two small British Museum specimens (82-92 mm S.L.) from Herradura Bay, just north of Antofagasta, clearly fit Hildebrand's diagnosis of *E. maculatum*. For the present, the two forms will be considered subspecies.

SYNONYMY. Hildebrand (*loc. cit.*) allied his *E. chilcae* most nearly to Steindachner's *Clupea notacanthoides*, but noticed slight differences in some proportions. Since it seems very likely that Steindachner had a Peruvian fish—and the description and figure suggest the large-headed Peruvian form—the slight differences noted by Hildebrand may well be attributable to faults in Steindachner's description, in which case the name *notacanthoides* should be used for the Peruvian subspecies.

Günther's type of *Clupea notacanthus* from Valparaíso (89.0 mm S.L., BMNH. 1848.6.14.42—one specimen now missing) is clearly the nominate form (head 30.6% of S.L.).

ILISHA Richardson, 1846

Ilisha Richardson, 1846, *Rept. Ichthyol. China Japan* : 306 (Type : *Ilisha abnormis* Richardson = *Alosa elongata* Bennett *vide* Whitehead, 1966).

Platygaster Swainson, 1838, *Nat. Hist. Animals*, 1 : 278 (Type : *Clupea africana* Bloch, designated by Swain, 1882, *Proc. Acad. nat. Sci. Philad.* : 280) ; *ibidem.*, 1839, 2 : 186, 294 (name preoccupied in Hymenoptera).

Zunasia Jordan & Metz, 1913, *Mem. Carnegie Mus.*, 6 (1) : 7 (Type : *Pristigaster chinensis* Basilewski = *Ilisha elongata*, see below).

Pseudochirocentron Miranda-Ribeiro 1923, *Comm. Linhas Telegr. Estrat. Matto Grosso Amazonas*, 58 : 8 (Type : *P. amazonicum* Miranda-Ribeiro).

Euplatygaster Fowler, 1934, *Proc. Acad. nat. Sci. Philad.*, 85 : 246 (Type : *Pellona brachysoma* Bleeker = *Ilisha indica*, see below).

At present, the genera *Ilisha* and *Pellona* are separated solely on the presence of a toothed hypo-maxilla in the latter (replacing the ligament connecting the tip of the pre-maxilla to the ventral edge of the maxilla). The presence of a toothed hypo-maxilla also separates the New World *Harengula* from the Indo-Pacific *Herklotsichthys* (subfamily Clupeinae), and the New World Pacific coast *Pliosteostoma* from the Atlantic coast *Odontognathus* (subfamily Pristigasterinae).

Having found a specimen of the *Ilisha-Pellona* complex with the hypo-maxilla present on one side and absent on the other, Myers (1950) preferred to await other evidence before splitting the genus *Ilisha*. Hildebrand (1964 : 415) also combined *Ilisha* and *Pellona*, but Berry (1964 : 729) split them again. No supporting evidence has yet been published, and I have been unable to find consistent differences in gill arches, fronto-parietal striation patterns, shapes of bones in the opercular and maxillary series, scutes or scales. Nevertheless, the separation of the species on a single, easily determined character (the hypo-maxilla) is useful and the generic level is preferred here.

It is unfortunate that the separation of *Pellona* from *Ilisha* does not coincide with a geographical separation. Most of the Indo-Pacific species are *Ilisha*, but *Pellona ditchella* Valenciennes has a hypo-maxilla ; conversely, most of the New World species are *Pellona*, but two species of *Ilisha* are recognized. I have been unable to find consistent differences between the groups of species from the two geographical areas.

The only comprehensive key to the species of *Ilisha* is that of Norman (1923). Subsequent keys are also unsatisfactory in view of re-examination of the type

material of Richardson, Bleeker, Valenciennes, Bloch and Steindachner (Whitehead, 1966 ; Whitehead *et al.*, 1966 ; Whitehead, 1967a; Whitehead, 1969b ; and the present study), coupled with the work of Myers (1950) and Hildebrand (1964). The following key is by no means definitive. It is intended as a summary of recent published and unpublished work ; there is still great need for a full revision of the Indo-Pacific species.

KEY TO SPECIES *Ilisha*

A. NEW WORLD

- 1 Post-pelvic scutes 6-7, total scutes 25-26 ; gillrakers 19-22 ; pelvic base nearer to anal origin than to pectoral base ; Atlantic drainage (Amazon of Brazil, Peru) 1. *I. amazonica* (Miranda-Ribeiro, 1923)
- 2 Post-pelvic scutes 12-14, total scutes 34-39 ; gillrakers 23-24 (and 11-12 on upper arch) ; pelvic base equidistant between anal origin and pectoral base or slightly nearer to the latter ; Pacific drainage and coasts (Costa Rica to Ecuador) 2. *I. furthii* (Steindachner, 1875)

B. EASTERN ATLANTIC

- 3. *I. africana* (Bloch, 1795)

C. INDO-PACIFIC

- 1 Anal origin in advance of or below middle of dorsal base ; pre-pelvic scutes 24-27 ; gillrakers 17-22 (Burma, Java, Borneo) 4. *I. pristigastroides* (Bleeker, 1852)
- 2 Anal origin below posterior half of dorsal base
 - a. Pre-pelvic scutes 22-27, post-pelvic 10-14 ; gillrakers 20-24
 - i Body deep, 37% of S.L. ; Borneo 5. *I. macrogaster* Bleeker, 1866
 - ii Body depth moderate, 30-34% of S.L. ; India, Borneo 6. *I. filigera* (Valenciennes, 1847)
 - iii Body slender, 24-28% of S.L. ; India to China 7. *I. elongata* (Bennett, 1830)
 - b. Pre-pelvic scutes 18-20, post-pelvic 7-9
 - i Body depth 37-41% of S.L. ; gillrakers 23-28 ; India to Singapore 8. *I. indica* (Swainson, 1839)
 - ii Body depth 32-34% of S.L. ; gillrakers 19-21 ; India to Singapore 9. *I. megaloptera* (Swainson, 1839)

There appear to be 39 nominal species referable to the genus *Ilisha*. To summarize recent work, these nominal species are listed (alphabetically) in Table 2, each name preceded by a number which allocates it to a species in the key given above. Following each entry is a reference (in parenthesis) to works in which type material or synonymies are discussed. Major difficulties surround species groups 5-7 and 8-9, in which body depth is used to separate species. Intraspecific variation in body depth is very poorly documented. The slender *I. elongata* is fairly distinctive, but the *macrogaster-filigera* complex may prove to be a single species. Similarly, the *indica-megaloptera* complex may also comprise a polytypic species in which variations in body depth and gillraker numbers can be correlated with habitat (purely freshwater, marine and intermediates).

The Swainson names *megalopterus* and *indicus*, based respectively on *Jangarloo* and *Ditchoe* of Russell (1803 : pl. 191 and pl. 192—reproduced in Whitehead, 1967a : pl. 8a, b), must be provided with neotypes. Russell's figure of *Jangarloo* shows a fish with 17+11 (? 18+12) scutes, a combination not yet found in Indo-Pacific specimens ; the count is presumed to have been 18+9 (i.e. section 2b of the key

above). Russell's figure of *Ditchoee* closely resembles Bleeker's figure and holotype of *Ilisha brachysoma* (Whitehead, *et al.*, 1966 : 98, pl. 13 (1)—from figure in *Atlas*), except that Russell gave an anal count of only 37 (47 rays in the holotype of *brachysoma*, but only 40 in the type of *Pellona micropus*). Even if Russell miscounted, a variation of 7 rays is rather large and it may later prove necessary to separate *I. brachysoma* from *I. micropus* (i.e. *I. indica*).

11. *Pellona furthii* Steindachner, 1875
= *Ilisha furthii* (Steindachner, 1875)

Pellona furthii Steindachner, 1875, *Sitzb. K. Akad. Wiss. Wien*, **70** : 388 (Bay of Panama, to 11½ zoll in length, i.e. 299 mm) ; *Idem*, 1875, *Ichthyol. Beitr.*, No. 1 : 14 (repeat).

TYPE MATERIAL

- a. LECTOTYPE, a fish of 201 mm S.L. (ca 260 mm tot.l.—caudal tips broken) *ex* Panama Bay in 1874, NMV.1110 [jar labelled I 1253 Steind. don. (typ)].
- b. PARALECTOTYPE, 1 fish, 215 mm S.L. (as above).
- c. PARALECTOTYPES, 2 fishes, 200–217 mm S.L., NMV.1106 (otherwise as above).
- d. PARALECTOTYPE, 1 fish, 210 mm S.L., NMV.1111 (otherwise as above).
- e. PARALECTOTYPE, 1 fish, 212 mm S.L., NMV.1872 (otherwise as above).
- f. PARALECTOTYPES, 2 fishes, 210–217 mm S.L., NMV.1114 (otherwise as above).

Another fish, 232 mm S.L., *ex* Panama in 1876 (NMV.1883) is not part of the type series.

DESCRIPTION. A fish, 201 mm S.L., 260 mm tot.l. (estimated, caudal tips damaged), LECTOTYPE, *ex* Panama Bay in 1874, in good condition apart from loss of caudal tips, NMV.1110.

Br.St. 6, D iv 13, P i 14, V i 5 (both), A iii 45, g.r. 11+23, scutes 22+13.

In percentages of standard length : body depth 36.4, body width 9.2, head length 24.7 ; snout length 6.8, eye diameter 8.0, upper jaw length 13.1, lower jaw length 13.3 ; length of pectoral fin 19.7, length of pelvic fin 6.4, length of anal fin base 45.0 ; pre-dorsal distance 45.7, pre-pelvic distance 43.4, pre-anal distance 60.0.

Body strongly compressed, its width 4 times in its depth, the latter 1½ times head length ; dorsal profile irregular, with slight "hump" behind occiput, ventral profile evenly convex, scutes prominent especially behind pelvic fin base.

Eye large, its diameter greater than snout length and 3 times in head length. Upper jaw reaching to just before vertical from eye centre ; median ⅓ of pre-maxillae toothless, a single series of minute conical teeth lateral to this ; no hypo-maxillae ; lower edge of maxillae with a series of fine teeth ; two supra-maxillae present, the 1st (anterior) slender and ½ eye diameter, the posterior with slender anterior shaft and expanded posterior part reaching almost to tip of maxilla (Figure 1). Lower jaw strongly projecting (7.5 mm beyond tip of snout), upper border rising, its height reaching half length of jaw just before midpoint ; a single series of 6–10 small conical teeth projecting inwards on either side of the symphysis.

Operculum with indentation along posterior border, its lower edge rising fairly steeply. Sub-operculum longer than deep, almost triangular. Entire gill opening covered by opercular series.

Pseudobranch present, exposed, a little under $\frac{1}{2}$ eye diameter in length, bearing about 25 filaments. Gillrakers slender, the longest $\frac{1}{2}$ eye diameter; gill filaments of anterior and posterior hemibranchs subequal, the longest 2.8 times in eye diameter. Four stubby gillrakers on posterior face of 3rd epibranchial.

Granular teeth present on tongue, palatines and endo- and ectopterygoids; no teeth on vomer.

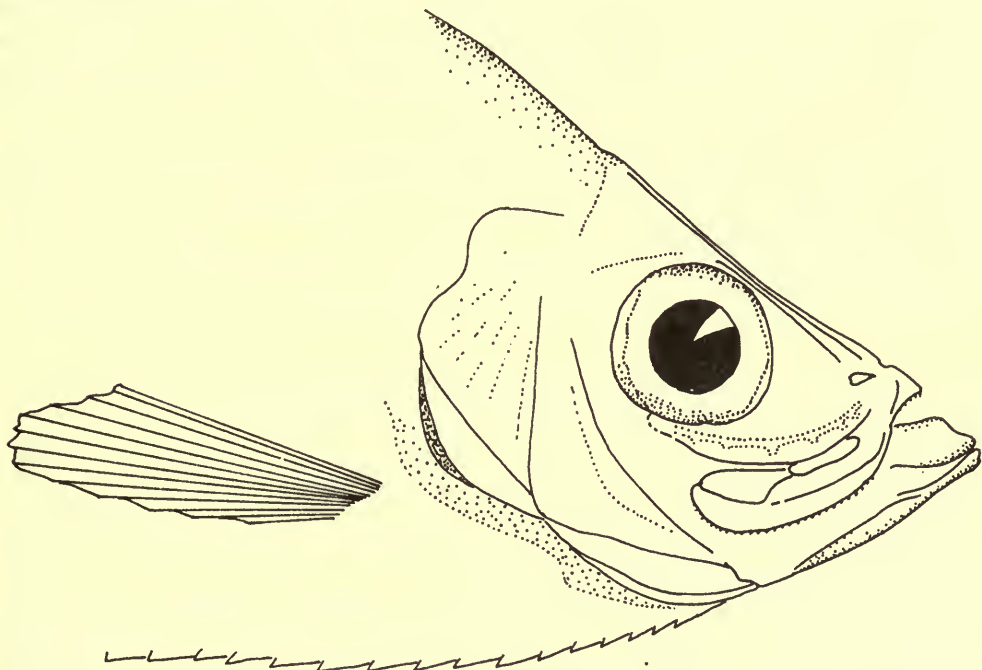


FIG. 1. *Pellona furthii* LECTOTYPE, 201 mm S.L., NMV.11110 (= *Ilisha furthii*).

Dorsal fin origin nearer to snout than to caudal base by 1 eye diameter; the first unbranched ray short and barely apparent. Pectoral fin tip broken but probably reaching to half-way along pelvic; axillary scale present, $2\frac{1}{4}$ – $2\frac{1}{2}$ times in length of fin; base of fin nearer to snout tip than to pelvic base by $\frac{1}{4}$ pupil diameter; base of fin covered by scales. Pelvic fin base equidistant between pectoral base and anal origin; no axillary scale present (? lost). Anal origin nearer to caudal base than to snout tip by 1 eye diameter.

Scales partly lost, posterior (exposed) border with faint signs of erosion and some small radiating striae (especially in posterior scales); unexposed portion of scales with up to eight convex striae, all interrupted at centre of scale except the most posterior.

Colour: upper 1/10 of body brown, remainder of flanks silvery; tip of pectorals and tips of posterior dorsal rays speckled brown.

IDENTIFICATION. The absence of a toothed hypo-maxilla in *Pellona furthii* was not unexpected. Norman (1923a) originally placed this species in his genus *Neosteus* (= *Pellona*) implying the presence of this bone, but assigned it to *Ilisha* when he had examined material (Norman, 1923b). Hildebrand (1946 : 91, footnote) could find no hypo-maxilla in six specimens from the Gulf of Guayaquil and, recognizing Norman's separation of *Pellona* from *Ilisha* on this character, placed his specimens in *Ilisha*.

Following the synonymy put forward by Myers (1950 : *Ilisha iquitensis* and *I. apapae* synonyms of *Pseudochirocentrodon amazonicum*), Berry (1964 : 729) deduced that there is a single species of *Ilisha* in the Western Atlantic drainage area of South America, *Ilisha amazonica* (Miranda-Ribeiro). No Western Atlantic specimens of *Ilisha* are in the British Museum collections, but *I. amazonica* is clearly distinct from *I. furthii* of Pacific coasts according to the descriptions of Hildebrand (1948 and 1964 : 421) and Myers (1950). The differences are shown in the key given above (p. 21).

Scute and some gillraker counts were made on the following seven British Museum specimens and the results incorporated in the key, together with counts for the types of *P. panamensis* (see below).

- a. 4 fishes, 160–201 mm S.L., ex Guayas River, Ecuador, BMNH.1938.11.18.1–4.
- b. 3 fishes, 216–238 mm S.L., ex Panama, BMNH.1938.5.15.305–7.

**12. *Pellona panamensis* Steindachner, 1875
= *Ilisha furthii* (Steindachner, 1875)**

Pellona panamensis Steindachner, 1875, Sitzb. K. Akad. Wiss. Wien, **70** : 389 (Panama) ; *Idem*, 1875, Ichthyol. Beitr., No. 1 : 15 (repeat).

TYPE MATERIAL. LECTOTYPE, a fish of 280 mm S.L. (365 mm tot.l.), ex Panama, NMV.1887 (labelled 1874–I/909– pt. a.).

PARALECTOTYPE, a fish of 265 mm S.L., ex Panama, NMV. 1890 (labelled 1874–I/909– pt.).

There is a third, non-typical, specimen of 258 mm S.L., ex Tumbez, coll. Stokm., NMV.1886.

DESCRIPTION. Two fishes, 280 and 265 mm S.L., LECTOTYPE and PARALECTOTYPE, ex Panama, in fair condition, caudal tips broken, many scales lost, occipital region dissected in paralectotype, NMV.1887 and 1890. (Figures for lectotype cited first).

Br.St. 5 (6), D iii 13 (14), P i 14 (14), V i 6 (6), A iii 49 (47), g.r. 11+24 (11+24), scutes 24+13 (23+13).

In percentages of standard length : body depth 32.6 (32.0), body width 8.7 (9.1), head length 26.0 (26.1) ; snout length 7.4 (6.9), eye diameter 7.4 (7.6), length of upper jaw 13.5 (13.1), length of lower jaw 14.2 (13.9) ; pectoral fin length 17.8 (16.7), pelvic fin length 5.9 (6.0), length of anal base 34.4(41.3) ; pre-dorsal distance 49.0 (48.7), pre-pelvic distance 46.0 (45.7), pre-anal distance 62.7 (63.7).

These two specimens differ from the type of *Ilisha furthii*, a smaller fish (201 mm S.L.), only in the more slender body (32.0–32.6 ; cf. 36.4), less convex belly profile,

slightly shorter pectoral fins (16.7-17.8 ; cf. 19.7) which do not reach the pelvic fin base, and shorter anal fin base (34.4-41.3 ; cf. 45.0). The latter is surprising, especially since the lectotype of *P. furthii* has fewer anal finrays, but there seems to be no justification for separating Steindachner's *P. panamensis*, as Norman (1923b) also concluded.

PELLONA Valenciennes, 1847

Pellona Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 300 (Type : *Pellona orbignyana* Val., designated by Gill, 1861, *Proc. Acad. nat. Sci. Philad.* : 38).

Neosteus Norman, 1923, *Ann. Mag. nat. Hist.* (9) **11** : 17 (Type : *Pellona ditchela* Valenciennes by subsequent designation of Norman, *Zool. Rec. Pisces* for 1923 : 25).

As in the case of *Ilisha*, the species of *Pellona* are very much in need of revision. The work of Hildebrand (1964) and examination of the status of the two Valenciennes species, *P. castelnaeana* and *P. flavipinnis* (Whitehead, 1967a : 106-110), can be summarized in the following key.

- I INDO-PACIFIC AREA ; scutes 18-19+8 ; anal iii-iv 32-24 ; gillrakers on lower part of 1st arch 23-25 1. *P. ditchela* Val., 1847
- II NEW WORLD
- A. Post-pelvic scutes 10-14 ; anal iii 32-37
1. Gillrakers on lower part of 1st arch 12-14 (Amazon system) 2. *P. castelnaeana* Val., 1847
2. Gillrakers on lower part of 1st arch 23-31 (as above but also from Surinam and Paraná) 3. *P. flavipinnis* Val., 1837
- B. Post-pelvic scutes 5-7 ; g.r. 23-25
1. Anal iii 33-39 (Atlantic coasts from Panama to southern Brazil) 4. *P. harroweri* (Fowler, 1917)
2. Anal iii 42 (single specimen from Newport, Rhode Island) 5. *P. narragansetae* (Fowler, 1911)

Pellona ditchela, the single Old World species, not only is inseparable from the New World species on any feature that could be regarded as of generic or subgeneric importance, but is so close to *Pellona harroweri* of Costa Rican and Brazilian waters that separation of the two is very difficult. Since the only pristigasterine linking these two regions is a species of *Ilisha* (*I. africana* of West Africa), it might be assumed that *Pellona ditchela* and *P. harroweri* are isolated relicts from a formerly much wider distribution of *Pellona*. Speciation in the Indo-Pacific may have been held back by competition from the more numerous species of *Ilisha*, whereas in the New World it is *Pellona* that appears to have speciated at the expense of *Ilisha*. The possibility cannot be ruled out that the combination of scute, anal finray and gillraker counts that characterizes *P. ditchela* and *P. harroweri* and distinguishes them from all other species may have been arrived at independently in the two species.

The use of gillraker numbers to separate *P. castelnaeana* (12-14) from *P. flavipinnis* (23-31) seems justified by the discontinuity shown in Table 3 and Figure 2. In an earlier paper (Whitehead, 1967a : 110) the low gillraker count in the smaller syntype of *P. castelnaeana* appeared to be the only exception to a general trend of reduction in number in larger fishes. Inclusion of the low gillraker counts found in three

specimens (220–275 mm S.L.) of *P. altamazonica* by Hildebrand (1964 : 418) and the high counts found in large fishes from the Guianas, however, suggests that there are two species, each with fairly constant numbers of gillrakers. A "slight" difference was found in the length of the pectoral axillary scale relative to fin length between the two species (Whitehead, 1967a : 110), but the relationship appears to be allometric and overlap occurs.

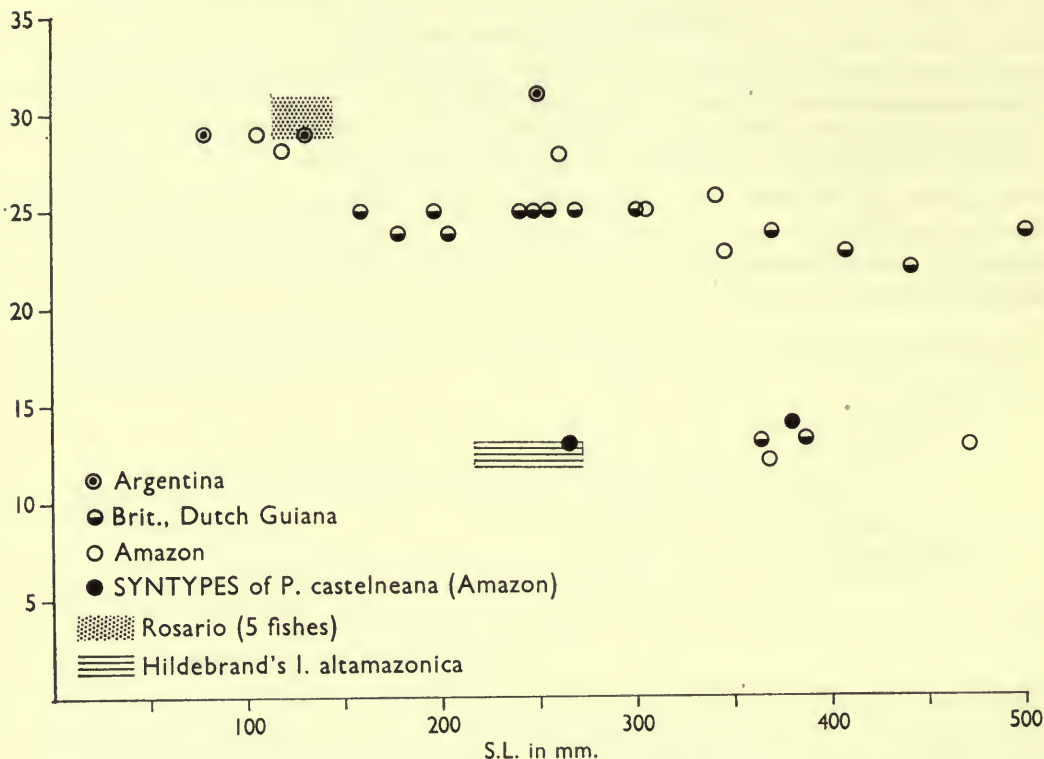


FIG. 2. Gillraker counts (lower arm, 1st arch) in specimens of *Pellona flavipinnis* (upper series) and *P. castelneana* (lower series). See Table 3, p. 44.

As Hildebrand (1964) supposed, *P. narragansetae* (known only from the holotype from Newport, Rhode Island, i.e. well outside the recorded range of the genus) was probably a stray and its separation from *P. harroweri* is perhaps not justified.

The following specimens have been labelled types of what appear to be MS. names never published by Steindachner.

"*Pellona staudingeri*"

= *Pellona flavipinnis* (Valenciennes, 1837)

A fish of 118.2 mm S.L., ex Iquitos (Peruvian Amazon), NMV.1112 (labelled 1884 I 300 a TYPE?).

A fish of 105.0 mm S.L., same locality, NMV.1893 (labelled I 1884 300).

The specimens have iii 34–iv 33 anal rays, 15+28 and 16+29 gillrakers, and 20+12 scutes. They are clearly *Pellona flavipinnis*, the high gillraker count distinguishing them from *P. castelnaeana* according to the key given here.

“ *Pellona macrolepis* ”
= *Pellona flavipinnis* (Valenciennes, 1837)

A fish of 340 mm S.L., *ex* Teffé (middle Amazon), NMV.1101 (labelled 1874—I, TYPE?).

This specimen has iii 37 anal rays, 14+26 gillrakers and 23+13 scutes. This high gillraker number reinforces the impression that there is no reduction in large fishes (Figure 2).

ODONTOGNATHUS Lacepède, 1800

Odontognathus Lacepède, 1800, *Hist. Nat. Poiss.*, **2** : 220 (Type : *Odontognathus mucronatus* Lacepède, 1800).

Gnathobolus Schneider, 1801, *Syst. Ichthyol. Blochii*, **2** : 556 (Type : *O. mucronatus* Lacepède).

Odontognathus is separated from the rather similar *Opisthopterus* Gill by its much longer maxilla (to gill opening or beyond ; cf. to vertical from eye centre in *Opisthopterus*). Berry (1964 : 729) showed that the maxilla exhibits positive allometry with standard length, and that in *Odontognathus* of 55–75 mm the elongation has already begun ; by 100–110 mm the tip of the maxilla has reached the opercular margin. Both genera lack pelvic fins but are otherwise similar to *Ilisha*.

Three species of *Odontognathus* are currently recognized and can be distinguished by the following key.

- 1 Scutes interrupted in area below pelvic fin base ; scutes with a single spine, outer margin not serrated ; anal rays 71–82 (Guianas to Trinidad) 1. *O. mucronatus* Lacepède, 1800
- 2 Scutes in continuous series ; outer margin of posterior scutes with 2–8 serrations
 - a. Anal rays 58–62 ; scutes 25–27 ; dorsal origin over about 16th anal ray (Trinidad to Costa Rica). 2. *O. compressus* Hildebrand, 1923
 - b. Anal rays 65–68 ; scutes 29–30 ; dorsal origin over about 25th anal ray (Pacific coast of Panama) 3. *O. panamensis* (Steindachner, 1876)

13. *Pristigaster (Odontognathus) panamensis* Steindachner, 1876
= *Odontognathus panamensis* (Steindachner, 1876)

Pristigaster (Odontognathus) panamensis Steindachner, 1876, *Sitzb. K. Akad. Wiss. Wien.*, **74** : 72 (Panama) ; *Idem*, 1876, *Ichthyol. Beitr.*, No. 5 : 24 (repeat).

TYPE MATERIAL. HOLOTYPE, a fish of 179.0 mm S.L., *ex* Panama, NMV.4626 (labelled 1874 I 2198 Steind. don.).

DESCRIPTION. A fish, 179.0 mm S.L. (204 mm tot.l., estimated), HOLOTYPE, *ex* Panama, in fair condition but tips of dorsal, anal and caudal fins damaged, scales mostly absent, NMV.4626.

Br. St. 4 (both), D i 11, P i 11, V (nil), A i 65, g.r. 8+20, scutes 30.

In percentages of standard length : body depth 25.3, body width 5.5, head length 17.3 ; snout length 4.6, eye diameter 4.8, upper jaw length 13.8, lower jaw length 8.0 (height 4.9) ; pectoral fin length 19.5, pelvic fin (absent), length of anal base 51.1 ; pre-dorsal distance 73.8, pre-anal distance 46.8.

Body strongly compressed, its width 5 times in its depth, dorsal profile "humped" at nape (? partly distorted) and concave over eye ; belly strongly keeled, scutes beginning on hind part of isthmus, prominent throughout, margins of 11th, 12th, 17th-30th scutes with 2-8 serrations (Figure 3b).

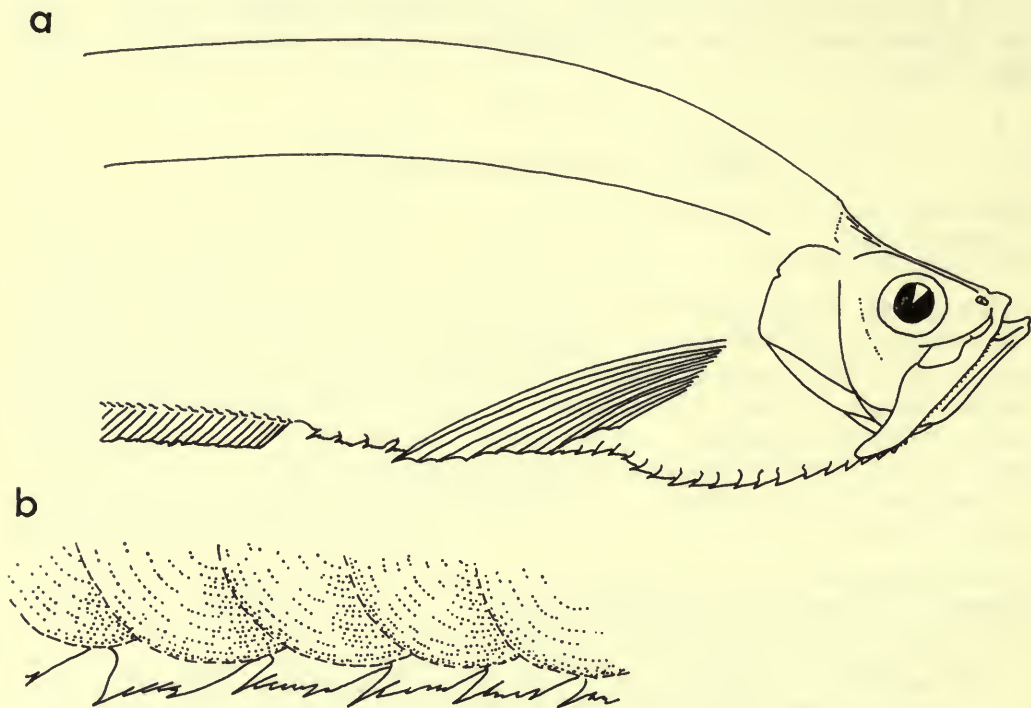


FIG. 3. *Pristigaster* (*Odontognathus*) *panamensis* HOLOTYPE, 179 mm S.L. NMV.4626 (= *Odontognathus panamensis*). a. Head and anterior half of body. b. Detail of serrated scutes behind pectoral fin tips.

Eye about equal to snout length, $3\frac{1}{2}$ times in head length. Upper jaw reaching to just beyond gill opening ; median $\frac{1}{4}$ of upper jaw edentulous, a single series of 10-12 fine, conical teeth on either side of this ; no hypo-maxilla ; lower edge of maxilla with a series of minute teeth reaching to posterior tip of bone ; two supra-maxillae present, the 1st (anterior) elongate kidney-shaped, 4.1 mm in length, the 2nd (posterior) with diamond-shaped expanded posterior part, 6.0 mm long and 3.9 mm deep, its posterior tip lying below vertical from eye centre ; maxilla depth rapidly decreasing behind tip of 2nd supra-maxilla, thereafter forming a slender blade (Figure 3a). Lower jaw slightly projecting, upper border rising rapidly, its height

reaching about $\frac{1}{2}$ of jaw length in first third of jaw ; a single series of about 5-6 small conical teeth on either side of symphysis.

Operculum with lower border rising at about 45° ; sub-operculum twice as long as deep. Gill opening entirely covered by opercular series. No cleithral lobe.

Snout with strong, blade-like mid-dorsal ridge dividing before eyes and extending to hind end of skull ; two smaller ridges on either side, enclosing a canal ; a median ridge at hind end of skull and two faintly striated fronto-parietal triangular areas.

Pseudobranch present, exposed, with 10 filaments, its length 5.5 mm ($\frac{3}{8}$ eye diameter). Gillrakers slender, the longest 4.4 mm ($\frac{7}{8}$ eye diameter) ; gill filaments shorter, the longest 3.3 mm. Two stubby gillrakers present on posterior face of 3rd epibranchial (none on 2nd arch).

Granular teeth present on tongue, palatines, ecto- and endo-pterygoids, the toothed area becoming ridged posteriorly in the latter.

Dorsal fin origin above 25th branched anal ray, twice as near to caudal base as to posterior margin of pre-operculum ; dorsal rays damaged at tips, but apparently only a single, rather broad unbranched ray ; dorsal base short, $\frac{3}{4}$ of eye diameter. Pectoral fin broad, its tip failing to reach anal origin by 2 eye diameters ; no axillary scale present. Pelvic fins absent. Anal fin base $\frac{1}{2}$ standard length, anal origin nearer to snout than to caudal base by $1\frac{1}{2}$ eye diameters.

Scales with slightly eroded posterior border and a few faint radiating striae ; unexposed portion without the main, uninterrupted vertical striation characteristic of clupeoid scales, but with 3-4 faint radiating striae not reaching centre of scale.

Colour : general light brown with two faint longitudinal silver lines, the first midlateral and the second a little above it ; cheek, operculum and belly silvery.

IDENTIFICATION. *Odontognathus panamensis* is very similar to *O. compressus* Hildebrand. Hildebrand (1923 : 194) found the dorsal origin slightly further forward in *O. compressus*, the anal fin base shorter and with fewer rays (58-62 ; cf. 65-68 in *O. panamensis*), and fewer ventral scutes (25-27 ; cf. 29). These are fairly small differences and a large sample of *O. panamensis* might bridge the discontinuity in finray and scute numbers. Both species have serrated scutes, which separates them from *O. mucronatus*, the latter further distinguished by a short non-scuted area below the pectoral fin base. *Odontognathus compressus* may yet prove to be merely an Atlantic subspecies of the Pacific *O. panamensis*.

Family ENGRAULIDAE

ANCHOVIELLA Fowler, 1911

Anchoviella Fowler, 1911, *Proc. Acad. nat. Sci. Philad.*, **63** : 211 (Type : *Engraulis per fasciatus* Poey).

Hildebrand (1943 : 108) redefined this genus to include species with a short and posteriorly rounded maxilla (Fowler had stressed the low number of gillrakers) ; Hildebrand recognized the subgenus *Amplova* Jordan & Seale for three species with exceptionally short maxillae, *A. balboae* (Jordan & Seale), *A. jamesi* (Jordan & Seale) and *A. brasiliensis* Hildebrand. Concentrating on maxilla length, Hildebrand failed

to recognize the nominal species *Stolephorus eurystole* Meek & Swain and *Anchoviella estanquae* Hildebrand as members of *Engraulis* (Whitehead, 1964b). *Anchoviella pallida* (Starks) belongs to another genus (see under *Anchovia*, p. 38), leaving 16 species of *Anchoviella*, distinguished mainly by rather small meristic and morphometric differences. In the majority of these species the number of gillrakers on the lower arm of the first arch is in the range 15–28; *A. balboae*, with 29–35, stands outside this range but examination of paratypical specimens of *Anchovia brevirostra* (= *A. balboae*) confirms this count and shows that this species is otherwise a fairly typical member of the *Amplova* group.

14. *Engraulis vaillanti* Steindachner, 1908
= *Anchoviella vaillanti* (Steindachner, 1908)

Engraulis vaillanti Steindachner, 1908, *Anz. Akad. Wiss. Wien*, **45**: 193 (Joazeiro and Barra on Rio São Francisco, Rio Grande do Norte, and Rio Preta, Brazil).

TYPE MATERIAL.

- a. LECTOTYPE, a fish of 62.7 mm S.L., ex Fazenda Ingaziera, labelled 1903 23/4b, NMV.1931.
- b. PARALECTOTYPES, 15 fishes, 39–68 mm S.L., from the same jar.
- c. PARALECTOTYPES, 16 fishes, 43.0–59.0 mm S.L., ex Lagoa Viana, labelled 1903, MNV.1928.
- d. PARALECTOTYPES, 6 fishes, 42.0–51.5 mm S.L., ex Lagoa do Porto, labelled 1903 (4)a, NMV.1929.
- e. PARALECTOTYPES, 3 fishes, 42.9–45.0 mm S.L., ex Rio Preto, labelled 1903a, NMV.1930.
- f. PARALECTOTYPES, 4 fishes, 39.2–42.0 mm S.L., ex Lagoa Viana and Lagoa do Porto, labelled 1903 31/3 4, NMV.1932.
- g. PARALECTOTYPES, 2 fishes, 39.2–40.6 mm S.L., ex Lagoa do Porto, labelled 1903c, NMV.1938.
- h. PARALECTOTYPES, 4 fishes, juveniles of 25.0–37.2 mm S.L., ex Barinha, labelled 1903 17/3 b, NMV.1936.

DESCRIPTION. A fish, 62.7 mm S.L. (75.3 mm tot.l.), LECTOTYPE, ex Fazenda Ingaziera, in fair condition but scales mostly lost, lower caudal lobe broken, NMV. 1931.

Br.St. 12, D iii 10, P i 12, V i 6 (both), A iii 20, g.r. 14+19.

In percentages of standard length: body depth 21.2, body width 9.2, head length 26.3; snout length 5.1, eye diameter 7.1, length of upper jaw 20.5, length of lower jaw 16.7; pectoral fin length 16.7 (axillary scale 8.7), pelvic fin length 11.6 (axillary scale 4.7), length of anal fin base 23.5; pre-dorsal distance 54.5, pre-pelvic distance 45.5, pre-anal distance 65.8.

Body fairly compressed, its width 2.4 times in its depth, the latter less than head length. Snout moderately prominent, a little less than eye diameter. Width of head above eye a little less than eye diameter. Upper jaw just reaching to mandibular articulation but not quite to anterior border of pre-operculum; tip of maxilla

evenly rounded, projecting only slightly beyond tip of 2nd (posterior) supra-maxilla ; the latter spatulate, tapering anteriorly and overlain half-way along its length by a plate-like 1st (anterior) supra-maxilla. Fine, close-set teeth on edge of maxillae, pre-maxillae and dentaries and minute teeth on palatines and ecto- and endopterygoids, but not on vomer.

Gillrakers fine, slender, the longest 2 mm long (about $\frac{1}{3}$ eye) and $1\frac{1}{4}$ times length of corresponding gill filaments ; 9 short rakers on posterior face of 3rd epibranchial. Pseudobranch present, exposed, about $\frac{1}{2}$ eye diameter. Isthmus brown (silvery in life?), sterno-hyoideus muscle not quite reaching to posterior border of branchiostegal membrane, the ventral edge of the urohyal exposed before this. A pair of crescentic posterior frontal fontanelles, together forming a triangle 1.6 mm long and 1.7 mm wide.

Dorsal fin origin equidistant between caudal base and posterior pupil border, i.e. nearer to caudal base by $1\frac{1}{2}$ eye diameters. Pectoral fin tips failing to reach pelvic base by $\frac{1}{2}$ eye diameter ; axillary scale present, almost $\frac{1}{2}$ length of fin. Pelvic fin base $\frac{2}{3}$ eye diameter before vertical from dorsal origin, nearer to pectoral base than to anal origin by $\frac{1}{2}$ eye diameter ; axillary scale present, $\frac{2}{3}$ length of fin ; inner rays of fins joined by membrane. Anal fin with low scaly sheath, its origin just behind vertical from last dorsal ray and $\frac{1}{2}$ eye diameter nearer to pectoral than to caudal bases.

Scales : unexposed portion with well-defined " shoulders " and 7-8 short horizontal striae, the two median striae meeting an irregular vertical striation ; exposed portion of scale with an irregular vertical striation followed by a reticular pattern of striae covering the rest of the posterior part of the scale ; hind border of scale not eroded. In some scales the reticular pattern extends forward and disrupts the (apparently) normal pattern of striae.

Colour : body brown with faint suggestion of silvery midlateral stripe ; a peppering of melanophores on snout, along entire dorsal profile, along posterior half of midlateral band (becoming heavier posteriorly) and on dorsal fin ; a dark vertical bar at base of caudal.

NOTE. Hildebrand (1943) had no specimens of *A. vaillanti*, but on the basis of Steindachner's description he distinguished the species by its high number of anal finrays, relatively few gillrakers and dorsal origin nearer to snout tip than to caudal base. As far as the lectotype is concerned, the latter is not true. Except for the posteriorly placed anal origin, *A. vaillanti* is close to *A. lepidenstole* (Fowler) but it has a more slender body. It also resembles *A. hubbsi* Hildebrand but has fewer gillrakers and a less prominent silver lateral band.

15. *Engraulis nattereri* Steindachner, 1879
= *Anchoviella nattereri* (Steindachner, 1879)

Engraulis nattereri Steindachner, 1879, *Sitzb. K. Akad. Wiss. Wien*, **80** : 174 (Pará, Brazil) ;
Idem, 1879, *Ichthyol. Beitr.*, No. 8 : 56 (repeat).

TYPE MATERIAL. Intensive search failed to produce the type, a specimen of 50 mm. It may have been sent with duplicates to another museum.

DESCRIPTION. (based on Steindachner's description).

Br.St. (n.r.), D 12, P(n.r.), V (n.r.), A 28 or 29, g.r. (n.r.).

Snout fairly long, reaching well beyond tip of lower jaw, 4.0 in head ; eye larger than snout, 3.6 in head. Maxilla tip nearly square, not quite reaching to mandibular articulation. Gillrakers moderately long, longest equal to eye diameter.

Dorsal fin origin slightly nearer to base of caudal than to tip of snout. Pectoral fin a little longer than postorbital distance, its tip reaching half-way along pelvic fin. Anal fin origin below middle of dorsal base.

Colour : silver midlateral band indistinct.

NOTE. Maxilla shape, number of anal finrays and position of anal origin all strongly suggest a species of *Anchoviella*. Hildebrand (1943 : 133), who had no specimens and relied solely on Steindachner's description, kept this species distinct. The rather long pectoral fins suggest *A. pallida* (Starks), but with no record of gill-raker number it seems best to follow Hildebrand for the moment.

ANCHOA Jordan & Evermann, 1927

Anchoa Jordan & Evermann, 1927, *Proc. Calif. Acad. Sci.*, (4) 16 (15) : 501 (Type : *Engraulis compressus* Girard).

This is the largest engraulid genus, with over thirty species recognized by Hildebrand (1943). The genus was originally distinguished from the very similar *Anchoviella* by the possession of more anal rays and gillrakers. Tables of anal ray and gillraker numbers given by Hildebrand (*loc. cit.*) show considerable overlap, however, and Hildebrand redefined the genus on the basis of the length of the maxilla :

Anchoa : tip of maxilla pointed, projecting well beyond tip of 2nd supra-maxilla and reaching beyond mandibular articulation, almost to gill opening.

Anchoviella : tip of maxilla truncate or bluntly rounded, projecting only slightly beyond tip of 2nd supra-maxilla and not reaching beyond mandibular articulation.

Three principal features distinguish both *Anchoa* and *Anchoviella* from *Engraulis* (Whitehead, 1964b ; summarized in Berry, 1964).

1. Posterior frontal fontanelles present (occluded in adult *Engraulis*).
2. Anal origin below or only just behind vertical from last dorsal ray (up to one eye diameter behind in *Engraulis*).
3. Pseudobranch short, equal to or less than eye diameter, not reaching to hyomandibular facet nor onto inner face of operculum, 15-25 pseudobranchial filaments (greater than eye, etc., 25-40 filaments in *Engraulis*).

Using these criteria, *Anchoviella eurystole* (Swain & Meek) and *A. estanquae* Hildebrand were recognized as members of *Engraulis* (Whitehead, 1964b : 882).

The redescription of the type of *Anchoa nasus* given below (p. 34) poses a further problem. In the three characters listed above, *A. nasus* approaches *Engraulis* while still maintaining the diagnostic feature of *Anchoa*, the long maxilla. The anal fin origin is not so far back as in *Engraulis*, the posterior frontal fontanelles appear to be excluded rather later in ontogeny and the pseudobranch is slightly shorter than

in *Engraulis*, but *A. nasus* is as close to *Engraulis* in these respects as it is to typical members of *Anchoa*. It has been noted (Whitehead, 1967a : 127) that three further species of *Anchoa* share these resemblances to *Engraulis*, viz. *A. lyolepis* (Evermann & Marsh), *A. argentivittata* (Regan) and *A. duodecim* (Cope) (B.M. specimens, including the type of *A. argentivittata*). Full revision of the anchovy genera may well support recognition of a separate genus or subgenus for these four species.

16. *Engraulis januarius* Steindachner, 1879
= *Anchoa januaria* (Steindachner, 1879)

Engraulis januarius Steindachner, 1879, *Stizb. K. Akad. Wiss. Wien*, **80** : 176 (ex harbour of Rio de Janeiro, Brazil) ; *Idem*, 1879, *Ichthyol. Beitr.*, No. 8 : 58 (repeat).

TYPE MATERIAL. LECTOTYPE, a fish of 51.4 mm S.L., ex Rio de Janeiro harbour, labelled " 1874 I 1566 ", NMV.2790.

PARALECTOTYPE, a fish of 54 mm S.L., from same jar.

DESCRIPTION. A fish, 51.4 mm S.L., LECTOTYPE, ex Rio de Janeiro harbour, in good condition, NMV.2790.

Br.St. 11, D iii 13, P i 12, V i 6, A iii 20, g.r. 21+27, scales *ca* 37 in lateral series.

In percentages of standard length : body depth 21.2, body width 7.8, head length 23.2 ; snout length 4.9, eye diameter 7.0, length of upper jaw 21.0, length of lower jaw 16.2 ; pectoral fin length 13.2, pelvic fin length 7.2, length of anal base 21.6 ; pre-dorsal distance 56.5, pre-pelvic distance 45.9, pre-anal distance 64.0.

Body compressed, its width 3 times in depth, the latter slightly less than head length. Snout a little shorter than eye diameter. Upper jaw reaching back beyond articulation of lower jaw and to vertical midway across pre-operculum ; lower edge of maxilla straight posteriorly, tip rounded, upper edge rounded to meet posterior tip of 2nd supra-maxilla ; the latter spatulate, tapering anteriorly ; anterior (1st) supra-maxilla slender, plate-like ; the maxilla projects 1.7 mm beyond the tip of the 2nd supra-maxilla. Teeth on pre-maxillae, maxillae and dentaries close-set, fine, very short ; fine teeth on palatines and ecto- and endo-pterygoids but not on vomer.

Gillrakers fine, slender, twice length of corresponding gill filaments and $\frac{3}{4}$ eye diameter ; 8 short rakers on posterior face of 3rd epibranchial. Pseudobranch present, partly invested in adipose tissue, with about ten short filaments, the length of the pseudobranch $\frac{1}{2}$ eye diameter. Isthmus silvery, sterno-hyoideus muscle extending forward almost to hind margin of branchiostegal membrane, the ventral edge of the urohyal exposed before this. Width of head over eye centre equal to eye diameter. A pair of triangular posterior frontal fontanelles, together 1.5 mm long and 1.4 mm at widest (posterior) point.

Dorsal fin origin equidistant between caudal base and posterior pupil border, i.e. nearer to caudal base than to snout tip by $1\frac{1}{3}$ eye diameters ; proximal half of fin invested in scaly sheath. Pectoral fin tips failing to reach pelvic base by $\frac{3}{4}$ eye diameter ; axillary scale present, $\frac{7}{10}$ length of fin. Pelvic fins small ; pelvic base $1\frac{1}{2}$ eye diameters before vertical from dorsal origin and equidistant between pectoral base and anal origin ; large axillary scale present (missing on right side), equal to fin

length. Anal fin origin below vertical from base of 8th branched dorsal ray and slightly nearer to caudal than to pectoral bases ; proximal half of fin invested in scaly sheath.

Scales : thin, apparently not caducous ; exposed portion with three complete irregular vertical striae, posterior edge slightly eroded ; unexposed portion with two short, incomplete vertical striae and two or three short radial striae from anterior edge of scale. The circulae on the unexposed portion of scale more widely spaced than those on the exposed portion ; the posterior $\frac{1}{3}$ of scale apparently without circulae.

Colour : body brown, with faint silvery midlateral stripe and silvery belly ; dark chromatophores forming diagonal line on upper part of caudal peduncle and a vertical bar below this.

NOTE. Hildebrand (1943) listed 36 species of *Anchoa*, for which he provided a complex and not altogether satisfactory key. Several species resemble *Anchoa januaria*, notably *A. mitchilli*, *A. parva*, *A. hepsetus*, *A. pectoralis* and *A. tricolor* (lectotype of the first fully described in Whitehead, 1967a : 127). Assessment of the importance of the small and mainly meristic differences separating these species must await full revision based on more material.

17. *Engraulis nasus* Kner & Steindachner, 1866

= *Anchoa nasus* (Kner & Steindachner, 1866)

(Plate 3a)

Engraulis nasus Kner & Steindachner, 1866, *Sitzb. K. Akad. Wiss. Wien*, **54** : 388, pl. 2 (17) (Chincha I., Peru).

Stolephorus cultratus Gilbert, 1892, *Proc. U.S. natl. Mus.*, **14** : 544 (Santa Margarita I., off Lower California).

SYNONYMY. Hildebrand (1943 : 70), who noted that the type of *Stolephorus cultratus* cannot now be found, allied that species with *Anchoa ischana* (Jordan & Gilbert) and *A. naso*. From Gilbert's description, however, *S. cultratus* is even closer to *Anchoa nasus*, differing only in minor respects (anal 20 ; cf. 21-27 ; maxilla "nearly to gill opening" ; cf. "not to margin of opercle"). Gilbert's species is perhaps a northern representative of *Anchoa nasus*.

TYPE MATERIAL. HOLOTYPE, a fish of 107.8 mm S.L., ex Chincha I., Peru, labelled Steindachner 1866 67, NMV.2837.

DESCRIPTION. A fish, 107.8 mm S.L. (132.6 mm tot.l.) HOLOTYPE, ex Chincha I., Peru, in good condition but scales mostly lost, NMV.2837.

Br.St. 13, D iii 13, P i 13, V i 6, A iii 20, g.r. 23+27.

In percentages of standard length : body depth 23.2, body width 8.9, head length 30.0 ; snout length 6.0, eye diameter 7.4, length of upper jaw 27.5, length of lower jaw 19.8 ; pectoral fin length 16.0 (axillary scale 9.5), pelvic fin length 10.2, length of anal base 22.6 (height of fin 12.2) ; pre-dorsal distance 56.2, pre-pelvic distance 45.8, pre-anal distance 69.0.

Body compressed, its width 2.6 times in its depth, the latter $\frac{3}{4}$ of head length.

Snout prominent, a little less than eye diameter. Upper jaw reaching back almost to hind margin of pre-operculum ; tip of maxilla pointed ; two supra-maxillae, the 2nd (posterior) spatulate, reaching to anterior margin of pre-operculum, the 1st (anterior) slender, plate-like ; maxilla projects 3.85 mm beyond tip of 2nd supra-maxilla. Anterior tip of lower jaw below vertical from anterior eye border. Teeth on entire lower edges of maxillae and on dentaries, fine and fairly close-set ; teeth on pre-maxillae even finer, granular teeth on palatines, ecto- and endo-pterygoids but not on vomer.

Gillrakers fine, slender, $1\frac{1}{4}$ times length of corresponding gill filaments and $\frac{3}{4}$ eye diameter ; 9 short, stubby rakers on posterior face of 3rd epibranchial. Pseudo-branch present, fully exposed, its length $1\frac{1}{2}$ eye diameters, about 30 filaments, the last two reaching onto the inner face of the operculum. Isthmus silvery, sternohyoideus muscle extending forward to posterior border of branchiostegal membrane, exposed portion of urohyal in front of this. Width of head over eye centre a little greater than eye diameter. Posterior frontal fontanelles occluded, the posterior tips of the frontals meeting in the midline and dividing only after reaching the supra-occipital ; frontal tips rounded posteriorly.

Dorsal fin origin equidistant between caudal base and posterior pupil border, i.e. nearer to caudal base than to snout tip by $1\frac{3}{4}$ eye diameters ; the few remaining scales suggest a scaly sheath to the base of the fin. Pectoral fin tips reaching $\frac{1}{2}$ eye diameter beyond pelvic base ; axillary scale present, $\frac{3}{4}$ length of fin. Pelvic fin base $1\frac{1}{4}$ eye diameters before vertical from dorsal origin, $\frac{1}{2}$ eye diameter nearer to pectoral base than to anal origin ; inner rays joined to each other by a membrane, overlain by two elongate scales ; no axillary scale found. Anal origin nearer to caudal than to pectoral base by $\frac{1}{2}$ eye diameter ; first unbranched anal ray a fraction behind vertical from base of last dorsal ray. Base of caudal with elongate scales reaching half-way along fin.

Scales : thin, many missing from anterior part of body but remainder firmly fixed ; anterior part of scale with distinct 'shoulders' and 7 horizontal striae whose ends bend towards the centre of the scale ; exposed portion of scale with (usually) seven vertical pairs of striae, the first two short, the third bent posteriorly half way along their lengths, the fourth short, the fifth meeting in the centre of the scale and the remaining two curved and either short or continuous across the scale (in many scales, possibly regenerated scales, the striae are reticulate, more or less disrupting the apparently normal pattern of striation).

Colour : upper $\frac{1}{3}$ of body light brown, remainder silvery, no sign of silver lateral stripe.

NOTE. The descriptions given by Hildebrand (1943) are insufficient to judge whether the resemblances of *A. nasus* to *A. ischana* and *A. naso* are superficial or whether they include the three features which *A. nasus* shares with *A. lyolepis*, *A. argentivittata* and *A. duodecim*, and which serve to distinguish these four species from all other members of *Anchoa* (see under genus, p. 32).

In the original description, the specimen was said to have a strongly convex dorsal profile and a nearly straight ventral profile (see Plate 3a). Hildebrand (1943 : 104) correctly assumed this to be a preservation artifact.

18. *Engraulis peruanus* Steindachner, 1879
 = *Anchoa nasus* (Kner & Steindachner, 1866)

Engraulis peruanus Steindachner, 1879, *Sitzb. K. Akad. Wiss. Wien*, **80** (ex Callao, Peru) ;
Idem, 1879, *Ichthyol. Beitr.*, No. 8 : 60 (repeat).

TYPE MATERIAL

- a. LECTOTYPE, a fish of 100.0 mm S.L., ex Callao, labelled 1874 I 1215 (pt.a) Steind. don., NMV.1965.
- b. PARALECTOTYPES, 3 fishes, 91.0–102.4 mm S.L., ex Callao, from same jar.
- c. PARALECTOTYPE, 1 fish, 94.8 mm S.L., ex Callao, labelled as above but (pt.d), NMV.1966.
- d. PARALECTOTYPES, 5 fishes, 79.3–97.6 mm S.L., ex Paraca Bay, as above, NMV.1964.
- e. PARALECTOTYPES, 2 fishes, 86.4–89.4 mm S.L., ex Callao, as above but (pt.), NMV.1967.
- f. PARALECTOTYPES, 2 fishes, 85.3–87.4 mm S.L., ex Callao, as above but (pt.c), NMV.1965.

DESCRIPTION. A fish, 100 mm S.L. (122.0 mm tot.l.), LECTOTYPE, ex Callao, in good condition but some scales lost, NMV. 1965.

Br.St. 13, D iii 13, P i 13, V i 6, A iii 23, g.r. 23+27.

In percentages of standard length : body depth 24.6, body width 8.3, head length 29.4 (width above eye centre 7.0) ; snout length 5.2, eye diameter 7.2, length of upper jaw 27.3, length of lower jaw 20.9 ; pectoral fin length 16.6 (axillary scale 9.8), pelvic fin length 10.0 (axillary scale 8.5), length of anal base 23.2 ; pre-dorsal distance 54.5, pre-pelvic distance 46.8, pre-anal distance 66.1.

In the remaining proportional and other features this specimen closely resembles the holotype of *Anchoa nasus* except that the anal fin origin is slightly further forward (below 11th branched dorsal ray ; cf. just behind last (13th) branched dorsal ray).

NOTE. Hildebrand (1943 : 102) placed *Engraulis peruanus* in the synonymy of *Anchoa nasus* on the basis of nine Steindachner specimens from Callao in the Museum of Comparative Zoology at Harvard. The description given here reinforces Hildebrand's view.

19. *Engraulis panamensis* Steindachner, 1875
 = *Anchoa panamensis* (Steindachner, 1875)

Engraulis panamensis Steindachner, 1875, *Sitzb. K. Akad. Wiss. Wien*, **72** : 589 (ex Panama) ;
Idem, 1875, *Ichthyol. Beitr.*, No. 4 : 39 (repeat).

TYPE MATERIAL

- a. LECTOTYPE, a fish of 113.2 mm S.L., ex Panama, labelled 1874 I 1149 (pt.) Steind., NMV.1970.
- b. PARALECTOTYPES, 2 fishes 112.7–125.0 mm S.L., ex Panama, from the same jar.

- c. **PARALECTOTYPES**, 2 fishes, 113.6–113.8 mm S.L., *ex* Panama, as above, NMV.1969.
- d. **PARALECTOTYPES**, 2 fishes, 109.2–114.9 mm S.L., *ex* Panama, as above, NMV.1972.
- e. **PARALECTOTYPES**, 2 fishes, 91.2–97.5 mm S.L., *ex* Panama, as above, NMV.1971.

DESCRIPTION. A fish, 113.2 mm S.L. (139 mm tot.l., estimated, caudal tips broken), **LECTOTYPE**, *ex* Panama, in fair condition, NMV.1970.

Br.St.12, D iii 11, P i 13, V i 6, A iii 31, g.r. 18+22.

In percentages of standard length : body depth 27.4 (width 6.0), head length 22.8 (width over eye centre 6.1) ; snout length 3.5, eye diameter 6.6, length of upper jaw 20.7, length of lower jaw 15.8 ; pectoral fin length 20.2 (axillary scale 5.7), pelvic fin length 9.2, length of anal base 35.2 ; pre-dorsal distance 56.8, pre-pelvic distance 41.2, pre-anal distance 56.3 ; caudal peduncle, length 12.4, depth 10.2.

Body strongly compressed, its width 4.5 times in its depth, the latter greater than head length. Head rather deep and dorsally (snout to supra-occipital) rather short. Snout not strongly prominent, almost half eye diameter. Upper jaw reaching almost to gill opening (right maxilla tip bent downward, left maxilla tip possibly lacking final mm) ; tip of maxilla apparently sharply pointed, projecting well beyond 2nd (posterior) supra-maxilla, the latter spatulate and tapering anteriorly ; 1st (anterior) supra-maxilla plate-like. Symphysis of lower jaw slightly before vertical from anterior eye border. Teeth along entire lower edges of maxillae and on dentaries, fine and close set ; teeth on pre-maxillae very small ; granular teeth on palatines, ecto- and endo-pterygoids and a patch of 4 small teeth on either side of the vomer ; a line of granular teeth along upper edge of ceratohyal.

Gillrakers fine, slender, $\frac{3}{4}$ eye diameter and twice length of corresponding gill filaments ; 6 short rakers on posterior face of 3rd epibranchial. Pseudobranch present, exposed, $\frac{3}{4}$ eye diameter. Isthmus silvery, sterno-hyoideus muscle extending forward just to posterior margin of branchiostegal membrane, urohyal exposed before this. Posterior frontal fontanelles exposed, crescentic, separated anteriorly by a wedge, the fontanelles 1.8 mm long and together 2.2 mm wide.

Dorsal fin origin almost 2 eye diameters nearer to caudal base than to snout tip ; a low scaly sheath along base. Pectoral fin tips reaching beyond pelvic base by $\frac{3}{4}$ eye diameter ; axillary scale present, short, about $\frac{1}{3}$ length of fin. Pelvic fin base equidistant between pectoral base and anal origin ; axillary scale ?lost ; inner rays of fin joined by membrane to body and perhaps originally to each other. Anal origin equidistant between caudal base and posterior border of pupil and directly below vertical from dorsal origin ; low scaly sheath present. Caudal peduncle almost as deep as long.

Scales : oval, deeper than wide, not firmly fixed, many missing ; anterior part of scale with ill-defined radiating striae and a single irregular vertical striation traversing scale ; exposed portion with 2–3 pairs of short vertical striae followed by numerous fine vertical striae increasingly connected to each other posteriorly to form a network ; posterior margin of scale apparently eroded. In many instances this pattern is disrupted by extensive reticulation of the striae.

Colour : body light brown except for silvery lateral stripe a little wider than pupil diameter ; opercular series silvery.

NOTE. This species is well defined in the key and description given by Hildebrand (1943) except that in his specimens the silvery lateral band on the body was "nowhere much broader than pupil."

The possession of vomerine teeth is not common in South American anchovies but occurs in some Indo-Pacific engraulids (e.g. *Thryssa*). The presence of denticulations along the upper edge of the ceratohyal, however, appears to be very rare in clupeoid fishes ; it is also found in large *Pterengraulis atherinoides* (135–190 mm S.L.—discrete tooth plates) and in *Anchoa spinifer* (over 70 mm S.L.—finely granular edge); in *Sardinops* there are numerous short plate-like but soft gillrakers.

ANCHOVIA Jordan & Evermann, 1896

Anchovia Jordan & Evermann, 1896, *Bull. U.S. natl. Mus.*, No. 47 (1) : 449 (Type : *Engraulis macrolepidotus* Kner & Steindachner).

This genus includes fishes which bear a strong resemblance to *Cetengraulis* (deep and compressed body, reduced jaw dentition and numerous close-set gillrakers which increase in number with size of fish). Members of *Cetengraulis* are clearly distinguished, however, by the broadly united branchiostegal membranes and the relatively long branchiostegal rays (about $\frac{1}{2}$ head length ; cf. $\frac{1}{3}$ – $\frac{1}{4}$ in other engraulid genera).

A further reason for considering *Anchovia* close to *Cetengraulis* is that these two genera share a peculiarity that appears to be of some systematic importance in the clupeoid fishes, namely the absence of gillrakers on the posterior face of the 3rd epibranchial. First noticed by Dr. Carl Hubbs (*in litt.*) in the New World species of *Engraulis* (*E. ringens*, *E. mordax*, *E. anchoita* and *E. juruensis*, but not in *E. eurystole* and *E. estanquae*, which belong in *Engraulis sensu stricto*), the absence of these gillrakers is now confirmed in *Hildebrandichthys* as well as in the Indo-Pacific engraulid genus *Coilia*. These rakers are also absent in *Gilchristella aestuarius* and *Ehirava malabaricus* (subfamily Pellonulinae) and *Clupea (Strangomera) bentincki* (subfamily Clupeinae).

The genus *Anchovia* contains five species in which the maxilla tapers to a point and projects markedly beyond the 2nd supra-maxilla, namely *A. macrolepidota* (Kner & Steind.), *A. magdalenae* Hildebrand, *A. rastralis* (Gilbert & Pierson), *A. clupeoides* (Swainson) and *A. nigra* Schultz. Three further species closely resemble the above (posterior gillrakers of 3rd epibranchial absent, etc.), but have a blunt maxilla not reaching beyond the mandibular articulation and barely projecting beyond the tip of the 2nd supra-maxilla, namely *A. surinamensis* (Bleeker), *A. pallida* (Starks) and *A. potiana* Schultz & Menezes. Since maxilla shape is the principal distinction between the genera *Anchoa* and *Anchoviella*, revisionary work may well justify splitting the genus *Anchovia*.

20. *Engraulis macrolepidotus* Kner & Steindachner, 1865
 = *Anchovia macrolepidota* (Kner & Steindachner, 1865)

(Plate 3b)

Engraulis macrolepidotus Kner & Steindachner, 1865, *Abh. K. Bayer Akad. Wiss.*, **10** : 21, pl. 3 (2) (Rio Bayano, Panama) ; Steindachner, 1876, *Sitzb. K. Akad. Wiss. Wien*, **72** : 587 (Panama).

TYPE MATERIAL

- a. LECTOTYPE, a fish of 104.7 mm S.L., *ex* Panama, labelled 1876 II/1P, NMV.2808.
- b. PARALECTOTYPE, a fish of 90.3 mm S.L., *ex* Panama, from the same jar.
- c. PARALECTOTYPE, a fish of 136.6 mm S.L., *ex* Acapulco, Mexico, labelled 1874 I 1736 Kn. St., NMV.2807.

DESCRIPTION. A fish, 104.7 mm S.L. (129.2 mm tot.l.), LECTOTYPE, *ex* Panama, in fair condition but scales mostly lost, NMV.2808.

Br.St. 14, D iii 12, P i 14, V i 6, A iii 27, g.r. 108.

In percentages of standard length : body depth 31.7 (width 7.8), head length 29.7 ; snout length 3.9, eye diameter 6.8, length of upper jaw 26.4, length of lower jaw 20.4 ; pectoral fin length 15.1, pelvic fin length 7.5, length of anal base 28.4 ; pre-dorsal distance 54.2, pre-pelvic distance 45.1, pre-anal distance 59.5.

Body compressed, its width 4 times in its depth, the latter a little greater than head length. Snout fairly pointed, a little over half eye diameter ; width of head above eye centre less than eye diameter. Upper jaw reaching a little beyond mandibular articulation to posterior margin of pre-operculum ; tip of maxilla pointed, projecting 4.0 mm beyond tip of 2nd (posterior) supra-maxilla ; the latter spatulate, tapering evenly anteriorly and overlain about halfway along its length by the smaller 1st (anterior) supra-maxilla. Fine denticulations along edges of maxilla and mandible becoming fainter anteriorly and not present on pre-maxillae ; fine teeth present along edges of palatines and ecto- and endo-ptyergoids, but not on vomer.

Gillrakers very fine and slender, the longest (7 mm) slightly exceeding eye diameter ; a double series of minute serrae along inner face of each raker ; no gillrakers present on posterior face of 3rd epibranchial. Gill filaments very short, $4\frac{1}{2}$ times in length of gillrakers. Pseudobranch present, exposed, equal to eye diameter, bearing 24 filaments. Isthmus silvery, sterno-hyoideus muscle dividing halfway along to expose the ventral edge of the urohyal, the latter covered by silvery tissue until shortly before the hind margin of the branchiostegal membrane. A pair of exposed posterior frontal fontanelles, 1.4 mm in length, lateral borders forming a sigmoid curve.

Opercular series (Figure 4) not covering gill opening ; operculum inclined at an angle of 45° ; sub-operculum almost triangular, the junction of the posterior and ventral margins produced into a distinct point.

Dorsal fin origin nearer to snout tip than to caudal base by $\frac{1}{2}$ eye diameter ; base of fin not invested in scaly sheath (? scales lost). Pectoral fin tips just reaching to pelvic fin base ; axillary scale present, $\frac{1}{2}$ length of fin, bearing a narrow flange along lower edge ; pectoral fins set low on body, below level of sub-operculum. Pelvic fins small ; pelvic base 1 eye diameter before vertical from dorsal origin and equidis-

tant between base of pectoral and anal origin ; no axillary scale (? lost) ; final rays of fin joined together in midline by a membrane and also similarly joined to body. Anal fin origin below middle of dorsal base (7th branched dorsal ray) and 2 eye diameters closer to pectoral base than to caudal base ; base of fin invested in scaly sheath.

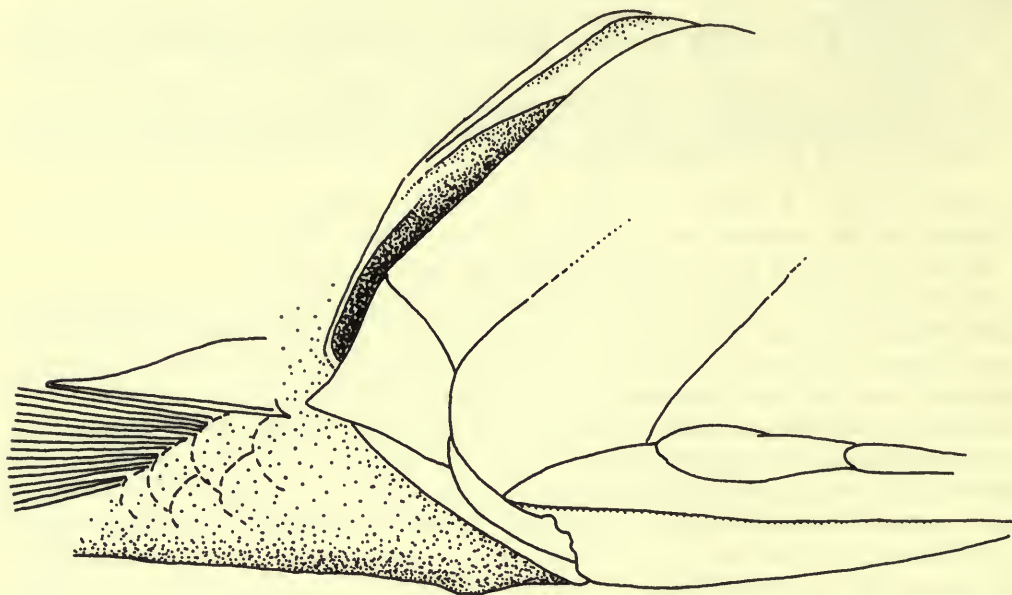


FIG. 4. *Engraulis macrolepidotus* LECTOTYPE, 104.7 mm S.L., NMV.2808 (= *Anchovia macrolepidota*). Opercular series (right side) showing characteristic shape of sub-operculum.

Scales : mostly missing ; exposed portion with an apparently random pattern of reticulated striae, unexposed portion with a single continuous curved striation preceded by up to five smaller radiating striae most of which fail to reach the centre of the scale.

Colour : upper $\frac{1}{4}$ of body brown, remainder silvery ; a dark line across bases of first few upper caudal rays ; very dark brown pigmentation on inner face of branchiostegal membrane.

LYCENGRAULIS Günther, 1868

Lycengraulis Günther, 1868, *Cat. Fish. Brit. Mus.*, **7** : 385 and 399 (Type : *Engraulis grossidens* Agassiz).

Hildebrand (1943) listed seven species of *Lycengraulis* and two further species have since been described, *L. limnichthys* Schultz and *L. simulator* De Plaza. In his key (p. 141), Hildebrand separated three species on the basis of their short, partly

rudimentary, gillrakers (*L. abbotti*, *L. barbouri* and *L. schroederi*). De Plaza (1962) noted a regression in the gillrakers of *L. simulator* with increasing size of fish but this did not reach the extreme condition found in the three species listed above. Hildebrand's specimens were all fairly large (148 and 205–237 mm S.L.), but he reported normal gillrakers in specimens of other species of a comparable size. It can be noted that small gillrakers are present on the posterior face of the third epibranchial in most species of *Lycengraulis* but are reduced or absent in specimens of *L. barbouri* at about 140 mm S.L. ; possibly this also occurs in the other species in which the gillrakers regress with age (*L. abbotti* and *L. schroederi*).

21. *Engraulis poeyi* Kner & Steindachner, 1865
= *Lycengraulis poeyi* (Kner & Steindachner, 1865)
(Plate 3c)

Engraulis poeyi Kner & Steindachner, 1865, *Abh. K. Bayer Akad. Wiss.*, **10** : 23, pl. 3, fig. 3
(Rio Bayano, Panama).

TYPE MATERIAL. Intensive search failed to produce any type material.

NOTE. *Lycengraulis poeyi* was well described by Hildebrand (1943 : 146), who placed it in the group with rather long and numerous gillrakers. It is the only member of the genus reported from the Pacific coasts of Central and South America ; it is well distinguished from the related *L. grossidens* and *L. olidus* of the Atlantic coasts by its high pectoral count (16–17 ; cf. 14–15), smaller jaw teeth and very short and blunt snout. Steindachner's description and figure (see Plate 3c) are adequate and the provision of a neotype is unnecessary at present.

TABLE 2

Alphabetical list of nominal species referable to the genus *Ilisha*. Numbers preceding name refer to senior synonyms listed in key (p. 21).

7. *abnormis* (*Ilisha*) Richardson, 1846, *Rept. Ichthyol. China Japan* : 306 (Whitehead, 1966 : 32).
7. *affinis* (*Clupea*) Gray, 1830, *Illustr. Ind. Zool.*, **1** : pl. 96 (2) (Whitehead, 1967a : 119).
3. *africana* (*Clupea*) Bloch, 1795, *Naturl. Aus. Fische*, **9** : 45, pl. 407 (Whitehead, 1969b : 268)
1. *amazonicum* (*Pseudochirocentron*) Miranda-Ribeiro, 1923, *Publ. Comm. Linhas Telegr. Estrat. Amazonas*, No. 58 : 8 (Myers, 1950 ; Hildebrand, 1964 : 241).
4. *amblyuropterus* (*Pellona*) Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 21 (Whitehead *et al.*, 1966 : 94).
1. *apapae* (*Ilisha*) Hildebrand, 1948, *Smithson. misc. Coll.*, **110** (9) : 3, fig. 2 (Myers, 1950).
8. *brachysoma* (*Pellona*) Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 22 (Whitehead *et al.*, 1966 : 100 ; Whitehead, 1967a : 116).
7. *chinensis* (*Pristigaster*) Basilewski, 1855, *Nouv. Mém. Soc. Nat., Moscow*, **10** : 243 (Fowler, 1941 : 662).
8. *ditchoa* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 313 (Whitehead, 1967a : 116).
3. *dolloi* (*Pristigaster*) Boulenger, 1902, *Proc. zool. Soc. London* : 271, pl. 30 (3) (Whitehead, 1967a : 112).
9. *dussumieri* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 316, pl. 596 (Whitehead, 1967a : 113).
7. *elongata* (*Alosa*) Bennett, 1830, *Mem. Life of Raffles* : 691 (Whitehead, 1967a : 119).
6. *filigera* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 322 (Whitehead 1967a : 117).
2. *furthii* (*Pellona*) Steindachner, 1875, *Sitzb. K. Akad. Wiss. Wien*, **70** : 388 (Hildebrand, 1946 : 91 ; see also p. 22).
3. *gabonica* (*Pellona*) Duméril, 1858, *Arch. Mus. Hist. nat.*, **10** : 259, pl. 3 (3) (Whitehead, 1967a : 112).
7. *grayana* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 315 (Whitehead, 1967a : 119).
8. *indicus* (*Platyaster*) Swainson, 1839, *Nat. Hist. Anim.*, **2** : 294 (Whitehead, 1967a : 114, 117).
3. *iserti* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 307 (Whitehead, 1967a : 112).
1. *iquitensis* (*Ilisha*) Nakashima, 1941, *Boll. Mus. Hist. Nat. "Javier Prado"*, **5** (16) : 66, fig. (Myers, 1950).
9. *kampeni* (*Pellona*) Weber & De Beaufort, 1913, *Fish. Indo-Austr. Arch.*, **2** : 87.
7. *leschenaulti* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 311 (Whitehead, 1967a : 118).

5. *macrogaster* (*Ilisha*) Bleeker, 1866, *Ned. Tijdschr. Dierk.*, **3** : 300 (Whitehead *et al.*, 1966 : 98).
9. *macrophthalmia* (*Platygaster*) Swainson, 1838, *Nat. Hist. Anim.*, **1** : 278 (*nomen oblitum*—Whitehead, 1967a : 115).
9. *megalopterus* (*Platygaster*) Swainson, 1839, *Nat. Hist. Anim.*, **2** : 294 (Whitehead *et al.*, 1966 : 103 ; Whitehead, 1967a : 114).
3. *melanota* (*Ilisha*) Derscheid, 1924, *Rev. Zool. Africaine, Bruxelles*, **12** : 278 (Whitehead, 1967a : 112).
8. *melastoma* (*Clupea*) Schneider, 1801, *Syst. Ich. Bloch.* : 427 (*nomen oblitum*—Whitehead, 1969b : 270).
8. *micropus* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 320 (Whitehead, 1967a : 116).
- ?8. *motius* (*Clupanodon*) Hamilton-Buchanan, 1822, *Fishes of Ganges* : 251, 383 (Whitehead, 1967a : 115).
7. *novacula* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 319 (Whitehead, 1967a : 121).
2. *panamensis* (*Pellona*) Steindachner, 1875, *Sitzb. K. Akad. Wiss. Wien*, **70** (1) : 389 (see p. 24).
8. *parva* (*Platygaster*) Swainson, 1839, *Nat. Hist. Anim.*, **2** : 294 (on Gray, 1834, *Illustr. Ind. Zool.*, **2** : pl. 109 (3), *Clupea motius*).
4. *pristigastroides* (*Pellona*) Bleeker, 1852, *Verh. Bat. Gen.*, **24** : 20 (Whitehead *et al.*, 1966 : 93).
9. *russellii* (*Pellona*) Bleeker, 1852, *Nat. Tijdschr. Ned. Ind.*, **3** : 72 (Whitehead *et al.*, 1966 : 101).
7. *schlegelii* (*Pellona*) Bleeker, 1854, *Nat. Tijdschr. Ned. Ind.*, **6** : 418 (Whitehead *et al.*, 1966 : 99).
7. *sinensis* (*Pristigaster*) Sauvage, 1881, *Bull. Soc. Philom. Paris*, (7) **5** : 107 (Whitehead, 1967a : 119).
4. *sladeni* (*Pellona*) Day, 1869, *Proc. zool. Soc. London* : 623.
8. *verticalis* (*Platygaster*) Swainson, 1838, *Nat. Hist. Anim.*, **1** : 278 (Whitehead, 1967a : 116).
7. *vimbella* (*Pellona*) Valenciennes, 1847, *Hist. Nat. Poiss.*, **20** : 317 (Whitehead, 1967a : 120).
6. *xanthopterus* (*Pellona*) Bleeker, 1851, *Nat. Tijdschr. Ned. Ind.*, **2** : 439 (Whitehead *et al.*, 1966 : 96).

TABLE 3

Gillraker counts in specimens of *Pellona castelnaeana* and *P. flavipinnis*.

<i>P. castelnaeana</i> (Amazon basin)	S.L.	gillrakers on lower arch
SYNTYPE MNHN.3705	380	14
SYNTYPE MNHN.3706	266	13
BMNH.1925.10.28.3	470	13
BMNH.1925.10.28.4	365	12
<i>P. altamazonica</i> (fide Hildebrand, 1964)	220-275	12-13
Guyana, Rupununi savannas.)	363	13
BMNH.1969.7.17.98		
<i>P. flavipinnis</i> (Amazon basin)		
BMNH.1897.7.17.19 (Amazon mouth)	345	23
NMV.1101 (Teffé)	340	26
BMNH.1929.11.18.2	305	25
BMNH.1869.5.21.51	260	28
NMV.112 (Iquitos, Peru)	118	28
	105	29
(Guyana, Surinam)		
BMNH.1934.9.12.2 (head only, 125 mm)	Approx. 500 mm	24
ZMA. (Marowijne R., Surinam)	438	23
	408	23
	370	25
BMNH. 1932.11.10.1	300	25
RMNH. (Surinam)	253	25
RMNH. 3344 (Surinam)	267	25
	248	25
BMNH. 1843.6.22.107	240	25
RMNH. 1675 (Surinam)	202	24
BMNH. 1936.5.6.1	197	25
BMNH. 1961.8.31.60	176	24
RMNH. (Surinam)	158	25
(Argentina)		
BMNH.1965.9.8.28 (Rosario)	250	31
BMNH.1878.5.16.2 (Buenos Aires)	130	29
BMNH.1965.9.8.22-27 (Rosario)	114-145	29-31
BMNH. 1969.11.25.146	78	29

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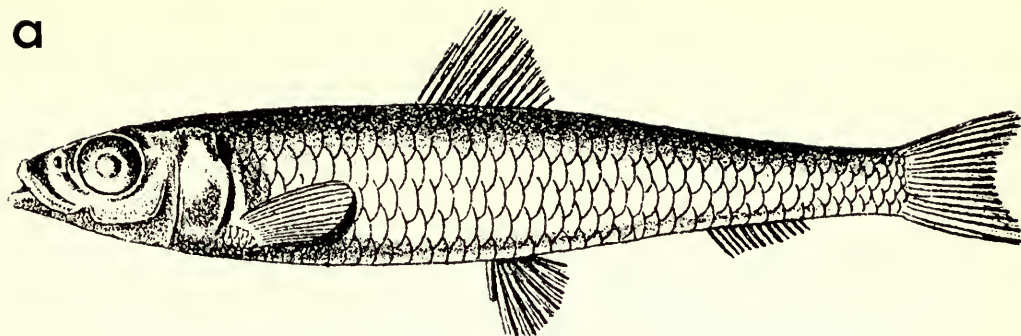
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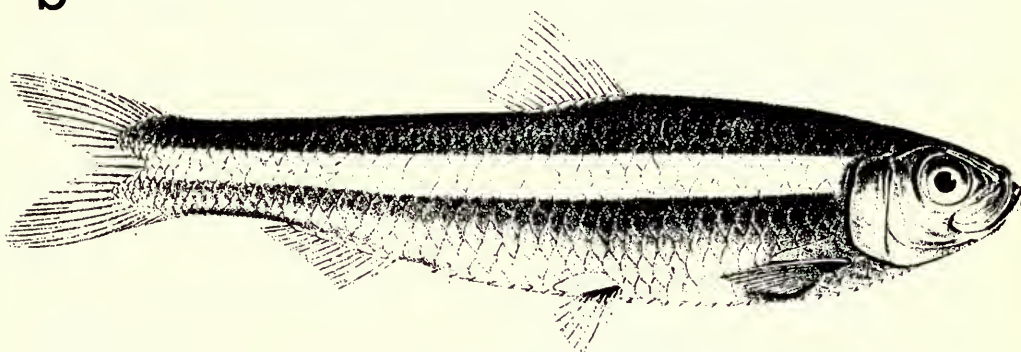
PLATE I

- a. *Alausa alburnus* Kner & Steind. (= *Spratelloides delicatulus*)
- b. *Pellonula bahiensis* Steind. (= *Rhinosardinia bahiensis*)
- c. *Alausa fimbriata* Kner & Steind. (= *Sardinops sagax sagax*)

a



b



c

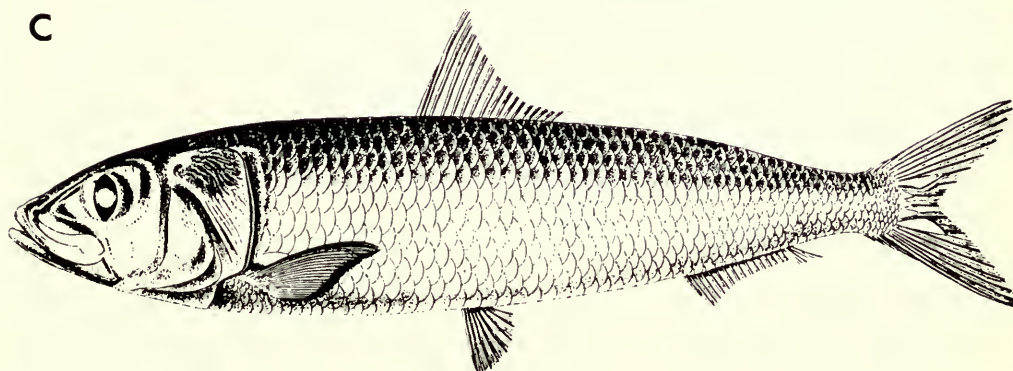
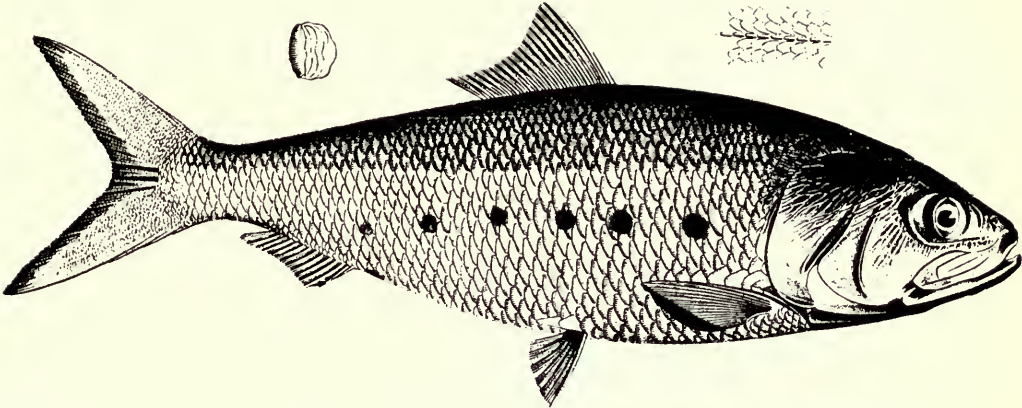


PLATE 2

- a. *Clupea setosa* Steind. (= *Ethmalosa fimbriata*)
- b. *Clupea notacanthoides* Steind. (= *Ethmidium maculatum notacanthoides*)

a



b

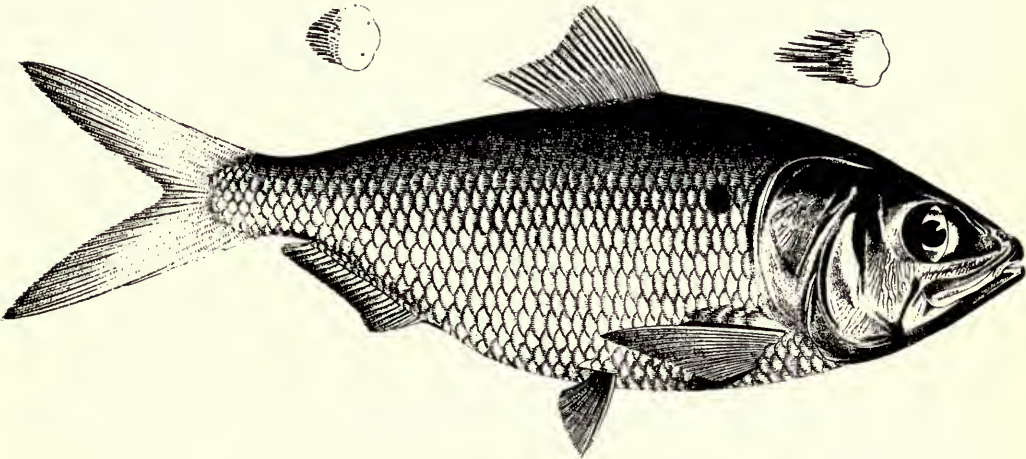
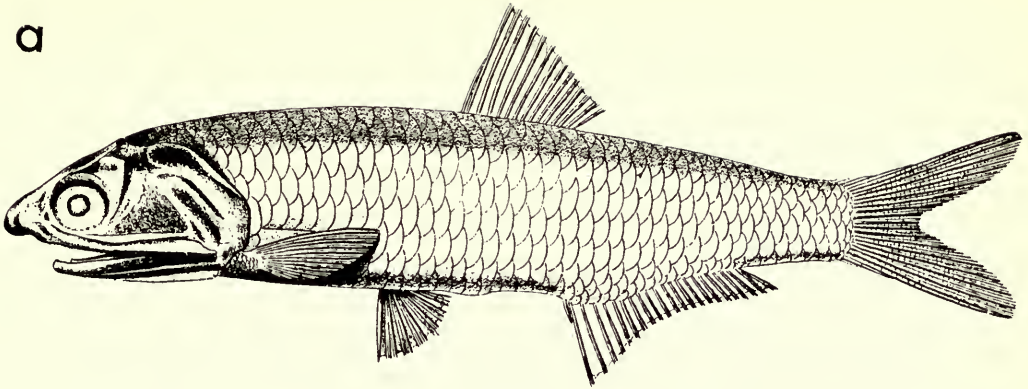


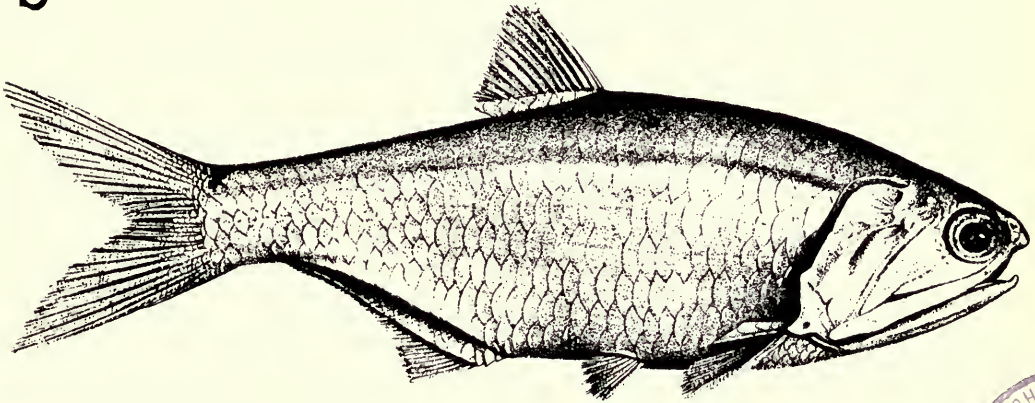
PLATE 3

- a. *Engraulis nasus* Kner & Steind. (= *Anchoa nasus*)
- b. *Engraulis macrolepidotus* Kner & Steind. (= *Anchovia macrolepidota*)
- c. *Engraulis poeyi* Kner & Steind. (= *Lycengraulis poeyi*)

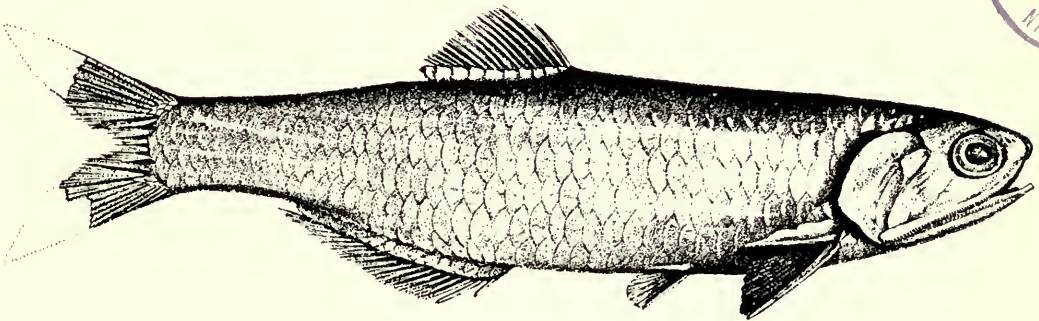
a



b



c



Printed in Great Britain by
Alden & Mowbray Ltd
at the Alden Press, Oxford

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SIPUNCULA AND ECHIURA
DESCRIBED BY

J. E. GRAY AND W. BAIRD

IN THE COLLECTIONS OF THE BRITISH
MUSEUM (NATURAL HISTORY)



MARY E. RICE
&
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BY

MARY ESTHER RICE

National Museum of Natural History,
Smithsonian Institution, Washington

and

✠ ALEXANDER CHARLES STEPHEN

Royal Scottish Museum, Edinburgh

Pp. 47-72 ; 3 Plates

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THE BULLETIN OF THE BRITISH MUSEUM
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*World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).*

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 9 November, 1970

Price £1.20

THE TYPE SPECIMENS OF SIPUNCULA AND ECHIURA DESCRIBED BY J. E. GRAY AND W. BAIRD

IN THE COLLECTIONS OF THE BRITISH MUSEUM (NATURAL HISTORY)

By MARY E. RICE & A. C. STEPHEN

SYNOPSIS

Type specimens of Sipuncula and Echiura of Gray (1828) and Baird (1868) in the collections of the British Museum (Natural History) were re-examined by the authors. Identifications were checked and, in most instances, the specimens were redescribed. Of the 23 type specimens, the specific names of the following were shown to be senior subjective synonyms of currently accepted names : *Siphunculus arcuatus* Gray 1828 [= *Phascolosoma lurco* (Selenka and de Man 1883)], *Phascolosoma perlucens* Baird 1868 [= *Phascolosoma dentigerum* (Selenka and de Man 1883)], *Themiste lageniformis* Baird 1868 [= *Themiste signifer* (Selenka and de Man 1883)], and *Aspidosiphon jukesii* Baird 1873 [= *Aspidosiphon corallicolus* Sluiter 1902]. Five were shown to have currently accepted valid names, one was a nomen dubium, and the remainder were junior synonyms to currently used names.

INTRODUCTION

DURING the course of the preparation of a monograph on the Sipuncula and Echiura, it became necessary to clarify the status of the several species described by Gray (1828) and Baird (1868 and 1873) since many were originally described mainly on external characters. Where these authors' specimens are still preserved in the collections of the British Museum (Natural History), it has been possible to check their identifications and, in most instances, to redescribe them. Because of the historic value of the specimens, only a minimum of dissection and manipulation was attempted ; hence complete redescrptions are not always provided in this report.

This study was initiated by the late A. C. Stephen of the Royal Scottish Museum and, after Dr. Stephen's death in 1966, it was completed by Mary E. Rice of the Smithsonian Institution.

Thanks are due to the Trustees, to Dr. J. P. Harding, Keeper of Zoology, and to Mr. R. W. Sims, Head of the Annelida Section, British Museum (Natural History) for permission to examine the specimens. Mrs. Carolyn Gast, scientific illustrator at the Smithsonian Institution, is gratefully acknowledged for her illustrations of the type specimens.

THE GRAY TYPES

Gray (1828 : 8, pl. 6, figs. 1, 4, 4a) described a series of sipunculans from the collections of the British Museum (Natural History) under the heading "Radiata",

family Siphunculidae. He included six species, four of which were described as new. These were : *Siphunculus dentallii*, *Siphunculus tuberculatus*, *Siphunculus arcuatus*, and *Themiste hennahi*.

Gray's brief diagnoses were in Latin, followed by a few comments in English, and they pertained only to non-specific external characters. Consequently, even though Gray's type specimens remained extant in the British Museum (Natural History), they were ignored by most subsequent authors. A re-examination of the specimens shows that the species names of *S. arcuatus* and *T. hennahi* are valid, whereas *S. tuberculatus*, demonstrated by Baird (1868) to be a junior primary homonym and re-named by him as *Phascolosoma grayi*, is here synonymized with *Phascolosoma noduliferum* Stimpson 1855. Specimens of *S. dentallii* are missing from the collection and apparently lost.

Siphunculus arcuatus Gray, 1828

Siphunculus arcuatus Gray, 1828, p. 8.

Phascolosoma arcuatum : Baird, 1868, p. 88.

HOLOTYPE : Reg. No. 1965. 25. 2

TYPE LOCALITY : India. Coll. Hardwicke.

DESCRIPTION : The specimen was preserved in a curved position with the introvert entirely retracted. It is in good condition with most of the internal organs well preserved, possibly because an incision had been made at one time in the body wall. The trunk measures approximately 100 mm in length and 20 mm at its maximum width. The retracted introvert is slightly longer than the trunk and is coiled and twisted within the body cavity. The basic colouration of the trunk is pale brown, although in the anterior third of the trunk there is an area of reddish-brown pigmentation. The papillae, distributed over the entire trunk, stand out as dark brown spots against the lighter background ; they are largest and most concentrated at the anterior and posterior extremities of the trunk (Figure 3, 3a-3c). The anterior and posterior papillae are pyramidal in shape, the largest measuring 0.8 mm in width and 0.5 mm in height in the posterior region ; the middle papillae are lower and more rounded, attaining a size of 0.5 mm in width and 0.24 mm in height. The platelets of the posterior and anterior papillae are dense and compact and in some cases more darkly pigmented toward the center of the papilla, whereas those of the middle papillae are more dispersed and evenly coloured (Figure 2). Surrounding the central opening of the papilla the platelets are smaller ; otherwise there is no obvious gradient in size of platelets.

The hooks are unidentate, strongly curved, with a clear central streak which is markedly wider at its basal extremity (Figure 2). The basal portion of the hook is diaphanous in nature and very much thinner than the remainder of the structure. Determination of the number of rows of hooks and number of tentacles would have required excessive manipulation of the retracted introvert of this historically valuable specimen ; hence, no observations were made on these characters. In distended areas of the body wall in the posterior half of the trunk, the cuticle is inflated into a series of small, thin-walled sacs (Figure 4). Upon dissection of the animal these sacs

appear to be vesicular expansions of the coelomic cavity into the body wall, extending through spaces between longitudinal and circular muscles. The integument covering the vesicles is markedly thinner than that of the remainder of the trunk.

Circular muscles, as well as longitudinal muscles, are divided into bundles. The longitudinal bundles show little anastomosis, numbering 18 at the level of the nephridiopores and 19 in the region of the posterior nephridia. The bundles of the circular muscles are smaller, more numerous, and less distinctive with frequent anastomoses. Two posterior retractor muscles originate in the posterior sixth of the trunk from longitudinal muscle bundles 2 and 3 and the two muscles soon join to form a single posterior retractor (Figure 1). The anterior retractors originate on either side of the ventral nerve cord, from longitudinal muscle bundle number 1 at the anterior end of the posterior quarter of the trunk near the level of the union of the posterior retractors. The anterior retractors soon join the posterior retractor to form a single retractor muscle (Figure 1).

The spindle muscle is attached at the posterior extremity of the trunk and after coursing anteriorly through the center of the intestinal coil and along the rectum, it attaches to the body wall immediately anteriorly to the anus. Prominent wing muscles fasten the anterior rectum to the body wall. Intestinal coils are numerous, but the exact number is difficult to ascertain because the coiling is somewhat erratic and parts of the gut are not well preserved.

The nephridia are approximately one-half as long as the trunk and are attached to the body wall for nearly their entire length. The nephridiopores open slightly anterior to the anus.

REMARKS : Gray's holotype of *Siphunculus arcuatus* corresponds with descriptions of *Phascolosoma lurco* (Selenka and de Man 1883, p. 61-63) in the following significant taxonomic characters : structure of hooks on introvert, form and distribution of papillae, fusion of four retractors into a single, long retractor muscle, and the number of longitudinal muscles.

In *Phascolosoma lurco*, as in the holotype of *Siphunculus arcuatus*, the origin of the anterior retractor muscles is ventral to that of the posterior retractors rather than the more common arrangement for sipunculans in which the posterior muscles originate ventral to the anteriors. One exception for *Phascolosoma lurco* was found in specimens examined by Lanchester (1905) in which both pairs of retractors originated from the same longitudinal line. The point of fusion of the four retractors in *Phascolosoma lurco* has been described differently by various authors. Selenka's figure depicts a fusion of the left anterior and posterior retractor muscles and a separate fusion of the two right retractors, resulting in one left and one right retractor which, after a short distance, unite to form a single muscle. Both Lanchester (1905) and Edmonds (1956), on the other hand, report that the four muscles fuse at about the same level to form one long retractor muscle. *Siphunculus arcuatus* presents a further variation : the two posterior muscles fuse to form one central muscle which courses anteriorly for a short distance and is then joined on either side by the left and right anterior muscles.

In *Phascolosoma lurco* as in *Siphunculus arcuatus*, the circular musculature shows a propensity for separation into bundles, although the bundles are not as widely spaced

nor as prominent or regular as those of the longitudinal muscles (Edmonds 1956, Selenka, de Man and Bülow 1883). In his description of *Phascolosoma lurco*, Selenka mentions small inflated areas in the body wall which may be comparable to the coelomic vesicles found in Gray's holotype.

In a synonymy of the two names, the specific name *arcuatus* has priority over *lurco*.

Siphunculus dentalii Gray, 1828

Siphunculus dentalii Gray 1828, p. 8 ; Johnston, 1833, p. 233-235, fig. 25.

TYPE LOCALITY : Coast of Yorkshire, in *Dentalium*. Coll. Clift.

This specimen is missing from the collection. It was not illustrated in Gray's report and his description which lists only general external characters is inadequate for a determination of the species involved. The locality of the specimen and its habitat in the shell of a *Dentalium*, suggest that it may have been *Phascolion strombus* (Montagu). However, Gray also described and figured a specimen of *Phascolion strombus* which he designated as *Siphunculus strombus* Mont. ; thus, it is obvious that he did not consider the two specimens to be the same, although the differences in his descriptions are non-specific, related mainly to shape and size of trunk and introvert.

In 1833, Johnston figured *S. dentalii* and elaborated on Gray's description, but he does not indicate whether he examined Gray's type specimen. Later authors (Selenka, de Man, and Bülow 1883, Gerould 1913, tenBroeke 1929) have placed *S. dentalii* Gray in synonymy with *Phascolion strombus* (Montagu).

Siphunculus tuberculatus Gray, 1828

Siphunculus tuberculatus Gray, 1828, p. 8 (non *Siphunculus tuberculatus* de Blainville, 1827).
Phascolosoma grayi (nom. nov.) Baird, 1868, p. 88.

HOLOTYPE : Reg. No. 1965.25.4

TYPE LOCALITY : Unknown

Gray (1828) described this specimen, to which he gave the name *Siphunculus tuberculatus*, as follows : " The body is conical and attenuated behind ; the trunk tubercular at the base, and nearly smooth at the apex. Length of the body $1\frac{1}{2}$ inch, its breadth $\frac{1}{4}$ inch ; length of the trunk $\frac{1}{2}$ inch ". In 1868 Baird pointed out that the specific name *tuberculatus* had been preoccupied by de Blainville in 1827. On re-examining Gray's specimen he concluded that it was different from de Blainville's species and renamed it *Phascolosoma grayi*, after Gray, who first defined the species. The type is now in rather poor condition. It had been previously dissected and most of the internal organs have been lost.

DESCRIPTION : The length of the body with fully extended introvert is approximately 60 mm, the maximum width 5 mm. The length of the introvert is slightly less than that of the trunk. The overall colour is a pale greyish yellow, somewhat darker at the base of the introvert and posterior end. The base of the introvert, the preanal region and the posterior quarter of the trunk are marked by a dense

accumulation of prominent, rounded, dome shaped papillae (Figure 11), the largest of which measures approximately 0.32 mm in diameter and 0.28 mm in height. In the middle region of the trunk the papillae are smaller, measuring as much as 0.20 mm in diameter and 0.08 mm high, and although distributed in a regular pattern they are more widely separated than at the extremities of the trunk. Platelets are arranged in a distinctive pattern in all papillae : a ring of dark brown platelets surrounds a clear central area and light-colored widely spaced platelets cover the remainder of the papilla (Figure 10). Roughly 20 rows of dark brown hooks encircle the anterior quarter of the introvert followed by numerous irregularly placed hooks. Simple in structure, the hooks are bent terminally and show a single clear central streak (Figure 9). Tentacles, although retracted, had been exposed by a previous dissection and 12 long filiform processes were counted.

The skin of the middle trunk is characterized by transverse wrinkling. Longitudinal wrinkling, weak and irregular in the middle trunk, is more pronounced in preanal and posterior regions.

Internally only the rectum, nerve cord, and nephridia remain in this incompletely preserved specimen. The nephridiopores and anus open at the same level. A broad wing muscle attaches the rectum to the body wall and the spindle muscle runs along the length of the rectum, inserting on the body wall immediately anterior to the anus. Only one nephridium, the left, is intact and it is attached for most of its length to the body wall with only the posterior end free. The longitudinal musculature is arranged in bundles which undergo considerable anastomosis, but at the level of the nephridiopores 25 bundles can be counted. The retractor muscles have been broken off and only remnants remain attached in the anterior introvert.

REMARKS : The characters which are still recognizable in this incomplete specimen agree closely with those of *Phascolosoma noduliferum* Stimpson 1855, as enumerated in a recent review of the species by Edmonds (1956). The number of muscle bundles falls within the range for *P. noduliferum* and the structure and distribution of the distinctive hooks and papillae are identical.

Although Baird listed *Phascolosoma noduliferum* in his monograph (1868), he failed to recognize the similarities between this species and the specimen designated by Gray as *Siphunculus tuberculatus*. Hence, after indicating that Gray's name was pre-occupied, Baird provided a new name, *Phascolosoma grayi*, whereas it appears that he should have synonymized the junior homonym with *P. noduliferum* Stimpson.

Themiste hennahi Gray, 1828

Themiste hennahi Gray, 1828, p. 8 ; Baird, 1868, p. 98 ; Stephen, 1964, p. 458 ; Amor, in press.

LECTOTYPE : Reg. No. 1965.16.1.

PARALECTOTYPES : Reg. No. 1965.16.2/5

TYPE LOCALITY : Peru. Coll. Rev. Hennah.

Stephen (1964), in a reclassification of the Sipuncula, demonstrated that the name *Themiste* Gray, 1828, was the senior synonym of the genus *Dendrostomum* Grube, 1858. Gray figured the tentacular crown of *Themiste hennahi*, the type species of *Themiste*

by monotypy, and clearly showed the dendritic nature of the tentacles but this paper was overlooked by Grube who erected the genus *Dendrostomum* for species with dendritic tentacles. Gray's original description of *Themiste hennahi*, quoted in full by Stephen as it had been printed in a thinly distributed publication of which few copies survive, was brief and inadequate by modern standards ; hence, a complete redescription of the specimens to which Gray gave the name *Themiste hennahi* is presented here. From the five specimens still intact at the British Museum (Natural History), Stephen (1964) designated one lectotype and four paralectotypes.

DESCRIPTION : The lectotype designated by Stephen (1964) is a fully extended specimen, measuring 70 mm in length to the base of the tentacles with a maximum width of approximately 15 mm (Figure 8). The introvert is one-fifth the length of the body and it is characterized by a relatively short smooth zone (5 mm) adjacent to the tentacular crown. The cuticle of the posterior introvert has become detached from the underlying epidermis, exposing the protruding canals of the epidermal glands (Figure 8a), and forming a wrinkled mass at the base of the introvert. No hooks or spines are apparent on the introvert. The predominant colour of the body is a pale grey, whereas that of the tentacles and smooth zone is light tan.

The well-extended dendritic tentacles arise from six primary stems (Figure 7). Between the bases of the tentacular stems are the six lappets or lips, membranous crescentic folds which form the margin of the mouth and demarcate the proximal boundaries of the six primary food grooves leading into the mouth from the tentacular stems. The dorsal lappet is distinguished by its large size and its proximity to the nuchal organ. The tentacular crown is asymmetric, the lateral tentacles exceeding both the dorsals and ventrals in length. The primary food grooves of the lateral stems are also longer, bifurcating at a greater distance from the mouth than the ventral and dorsal grooves.

The openings of the epidermal glands are distributed in a regular pattern over the surface of the trunk ; in the anal region the openings are in the form of slits and are situated on oblong elevations of the skin (Figure 8b). More posteriorly the openings approach a spherical shape ; in the middle of the trunk they are situated between transverse furrows of the skin, but no distinctive elevations are apparent (Figure 8c). In the posterior portion of the trunk the skin is marked by longitudinal as well as transverse furrows, resulting in small irregular rectangles within each of which is enclosed a gland opening. At the posterior extremity of the body the openings are elevated on dome-shaped swellings of the skin (Figure 8d). The position of the nephridiopores is slightly posteriorly to that of the anus.

Since the lectotype had not been dissected, it was left intact and the internal anatomy of this specimen was not studied. However, of the four paralectotypes, two had been previously dissected and the better preserved and more clearly dissected specimen was selected for the description of internal anatomy which follows (Figure 6). The introvert of this paralectotype was retracted and the length of the body without introvert was approximately 37 mm.

The musculature of the body wall is smooth and iridescent. A pair of wide, thickened retractor muscles originate on either side of the ventral nerve cord at the beginning of the posterior third of the trunk. The spindle muscle is not attached

posteriorly, but emerges anteriorly from the intestinal coil and, after giving off a short branch to the caecum, continues along the rectum, attaching to the body wall slightly posteriorly to the level of the anus. Three fixing muscles were observed (Figure 6). F_1 arises on the left side of the body in the anterior third of the trunk in a ventrolateral position and inserts on the oesophagus in the region where the contractile vessel breaks up into many blind vessels. The F_2 unfortunately had been broken in this specimen and its point of insertion was not determined; its origin is in a ventrolateral position on the left side of the body slightly posteriorly to the origin of F_1 . The fixing muscle F_3 is a short thick muscle which attaches the last ascending intestinal coil to the dorsal body wall.

The oesophagus is long, narrow, and thin-walled and, in this specimen it is looped under the right retractor (Figure 6). Running along the dorsal side of the oesophagus is the contractile vessel, enormously distended anteriorly. It is attached to the oesophagus for approximately one-fifth the length of the latter and at its posterior end it breaks up into many blind vessels or villi which ramify throughout the body cavity. Resembling strings of beads, these processes of the contractile vessel are marked by globular enlargements connected by thin, narrow, sometimes coiled strands. The intestine is wound into numerous coils (approximately 40 single coils), difficult to count with accuracy because of irregular winding and poor preservation in some parts. The wall of the gut is very thin and the ascending gut is filled with fine sand or mud particles. The beginning of the rectum is marked by the presence of a small caecum and in the anal region the rectum is attached to the body wall by broad wing muscles.

Two nephridia, more than half the length of the trunk, hang freely in the body cavity. The anterior portions of the nephridia are swollen and distended; the nephrostomes are small and simple. Nephridiopores open slightly posteriorly to the anus.

In addition to the lectotype and paralectotype described above, there are three remaining paralectotypes of *Themiste hennahi*. One of these is a small specimen which had been dissected; its tentacles are partially extended and the trunk, without the introvert, measures approximately 20 mm in length. In the other two paralectotypes the introvert is retracted and the approximate measurements of the lengths of the trunks are 45 mm and 40 mm.

REMARKS : The number of tentacle stems was recorded originally as five (Gray 1828). Stephen (1964), looking at the same specimen which he designated as the lectotype, reported Gray's count of tentacles to be in error, stating that "... there are only four tentacle stems, one shows a false dichotomy which misled Gray into thinking that there were five". A re-examination of this specimen by one of the present authors (Rice) has shown, in contradiction to the two previous reports, that there are six tentacular stems with six distinctive primary food grooves. The oral view of the tentacular crown illustrated in Figure 7 clearly shows the six primary stems, food grooves and lips. Gray figured a lateral view of the anterior end of this same specimen, but his view does not clearly delineate the number of tentacles. Perhaps the past discrepancy has been due in part to a failure to regard the number and position of lips. Moreover, the variation in length, size, and branching of the

tentacles and the differing lengths of the primary food grooves of the specimen prove to be confusing in any attempt to count tentacles. Another possible source of error in the interpretation of tentacular arrangement is the absence of one of the tentacles from the right ventral tentacular stem ; apparently it had been broken off at some time just beyond the point of the first bifurcation of the primary stem, and only the base of the tentacle and the beginning of the secondary food groove remain (Figure 7).

The two species *Dendrostomum peruvianum* Collin, 1892, and *Themiste hennahi* Gray were synonymized by Stephen in 1964. *D. peruvianum* has been recorded in the literature by two authors in addition to Collin (1892) : Fischer (1914) and Wesenberg-Lund (1955). As in the case of *T. hennahi*, reports of the number of tentacles of *D. peruvianum* are found to vary. Fischer (1914) reported five tentacle stems, whereas in the original description of the species Collin mentioned only four.

Collin (1892) described slightly raised papillae in the middle and posterior body of *Dendrostomum peruvianum* ; Fischer denied the presence of typical papillae, but nevertheless described dome-shaped elevations in the posterior body onto which the canals of the skin glands opened. Wesenberg-Lund (1955) reported an absence of projecting papillae, but described instead low circular papillae lying between the wrinkles of skin. In the Gray lectotype projecting papillae were not found in the middle of the trunk but in the posterior and anal regions the glands opened on elevated protuberances of the skin.

Oesophageal protuberances described by Collin were not seen by Wesenberg-Lund on the specimen which she identified as *Dendrostomum peruvianum*, nor were they observed in this study on the Gray paralectotype. As in Fischer's specimen of *D. peruvianum*, the caecum of the paralectotype of *T. hennahi* is found at the beginning of the rectum, not on the penultimate intestinal coil as described by Collin. Also varying from Collin's description, the F_3 fixing muscle of the paralectotype is attached to the last intestinal coil rather than the penultimate, and an F_4 fixing muscle is absent.

In other characters, published descriptions of *Dendrostomum peruvianum* agree essentially with the Gray specimens. The beaded structure of the villi of the contractile vessel, clearly evident in the Gray paralectotype, is described as characteristic of *D. peruvianum*.

Themiste hennahi also shows many similarities to the species described as *Dendrostomum zosteriolum* Chamberlin 1919 and *Dendrostomum schmitti* Fisher 1952. The possibility that these may all represent a single species remains to be determined by future studies.

THE BAIRD TYPES

In 1868 Baird published his monograph on the species of worms belonging to the subclass Gephyrea in the collections of the British Museum. In this he listed 142 species, including 18 descriptions of new species, 17 of which were sipunculans and one a priapulid. Later in a short paper published in 1873, he erected two additional species, *Aspidosiphon jukesii* and *Echiurus farcimen*. Baird's descriptions were short and based solely on external characters ; thus, they were inadequate for recognition

by later workers. In Appendix E of their monograph, Selenka, de Man and Bülow listed all of the new species described in 1868 by Baird with the exception of *Pseudo-aspidosiphon gracile* which they considered in the text. They examined six of Baird's type specimens, redescribing and retaining the names of four, and placing two other names in synonymy. The remainder listed in the appendix they considered to be insufficiently described and for some reason which remains unexplained they did not examine these specimens. No further attention seems to have been given to the specimens until Edmonds (1955, 1961), reporting on the sipunculans of Australia, redescribed three of Baird's types.

For this report, all of Baird's type specimens have been re-examined, the validity of the names is reviewed, and, where appropriate, they are relegated to the proper synonymy.

***Sipunculus aeneus* Baird, 1868**

Sipunculus aeneus Baird, 1868, p. 81.

Siphonosoma australe : Edmonds, 1961, pp. 217-220, 2 figs.

HOLOTYPE : Reg. No. 1952 : 10.8.

TYPE LOCALITY : New Zealand. Coll. Cuming.

This specimen was examined by Edmonds (1961) who redescribed it completely and referred it to *Siphonosoma australe* (Keferstein 1865). Following Baird's original description and previous to Edmonds' report, the name had appeared in the literature only twice : Selenka, de Man, and Bülow (1883) listed it in Appendix E of their monograph and Benham (1903) referred to it as a "species inquirenda".

***Sipunculus angasii* Baird, 1868**

Sipunculus angasii Baird, 1868, p. 80, pl. IX, fig. 1.

Sipunculus angasi : Edmonds, 1955, pp. 83-86, figs. 1-4.

SYNTYPES : Reg. No. 1864 : 12.13.3a/b.

TYPE LOCALITY : Port Lincoln, Spencer Gulf, South Australia. Coll. Angas.

In his description, Baird (1868) mentioned only non-specific external characters and the name was not used again in the literature until 1955 when Edmonds identified a large number of specimens from Australia as *Sipunculus angasi*. At that time Edmonds re-examined Baird's syntypes which he considered to be juveniles and described the internal anatomy of one of the specimens. *Sipunculus angasi* was regarded by Edmonds as closely allied to *S. robustus* Keferstein and *S. nudus* Linnaeus.

***Sipunculus deformis* Baird, 1868**

Sipunculus deformis Baird, 1868, p. 80-81, pl. ix, fig. 2.

Siphonosoma cumanense : Edmonds, 1955, p. 90-92.

HOLOTYPE : Reg. No. 1965.25.7.

TYPE LOCALITY : Sir Charles Hardy's Island, North Australia. Coll. Brookes.

Edmonds in 1955 gave a brief description of the internal anatomy of this specimen and considered it to be *Siphonosoma cumanense*. The only other time the name

Sipunculus deformis has appeared in the literature subsequent to Baird's description was in Appendix E of the monograph by Selenka, de Man and Bülow (1883).

***Sipunculus eximino-clathratus* Baird, 1868**

Sipunculus eximio-clathratus Baird, 1868, pp. 81-82.

HOLOTYPE : Reg. No. 1965.25.8.

TYPE LOCALITY : Philippine Islands. Coll. Cuming.

Baird's description was limited to external characters and he did not dissect the specimen. It is still in good condition, although a small part of the body wall had been damaged and the viscera at this point destroyed. A dissection was made by one of the authors (ACS) and a description of the internal anatomy is included below.

The specimen was preserved in a curved position with most of the introvert retracted. Measuring approximately 70 mm in length, the trunk is contracted in the mid-region but distended into bulbous expansions anteriorly and posteriorly. As pointed out by Baird, the skin is divided into rectangular areas by longitudinal and transverse furrows and the introvert is covered with triangular protuberances which point in a posterior direction.

Thirty-three longitudinal muscle bundles were counted in the anterior fifth of the trunk and about 30 in the middle. Four short retractor muscles originate quarter of the length of the trunk from the anterior end. The spindle muscle attaches to the body wall anterior to the anus ; a short distance posterior to the anus the characteristic " Buschel " organs occur. A caecum is present at the beginning of the rectum. The frons, or cerebral organ, is a simple flap of tissue with no obvious elaborations.

These characters correspond with those of *Sipunculus nudus* Linnaeus, a widely distributed tropical form.

***Phascolosoma aethiops* Baird, 1868**

Phascolosoma aethiops Baird, 1868, p. 90.

HOLOTYPE : Reg. No. 1839.12.26.46.

TYPE LOCALITY : St. Vincent, West Indies. Coll. Guilding (?).

In the monograph of Selenka, de Man, and Bülow (1883) the name *Phascolosoma aethiops* is listed in Appendix E and followed by the question " Ist ein Dendrostoma? ". Since there is no reason to believe that Selenka ever examined this specimen, it is probable that his question arises from Baird's description of the tentacles as " short and numerous " and his mistaken reference to " small black spines " on the introvert (Baird 1868).

DESCRIPTION : The holotype is in rather fragile condition and seems to have been either wholly or partially desiccated at some time. It was dissected by one of the present authors (ACS) and even with a minimum of interference the tentacular crown became detached.

The stout, thick trunk is 25 mm long and 8 mm at its maximum width ; the introvert is 5 mm in length without the tentacles. The tentacles are filiform, numerous,

and in a position dorsal to the mouth. Even though the tentacles were described by Baird as short, they measure as much as 3 mm in length which is a considerably greater relative length than that found in the majority of species of *Phascolosoma*.

The light brown skin is covered with numerous contrasting dark brown papillae. On the introvert the papillae are conical, resembling spines, although true spines, as cited by Baird, are lacking. Papillae on the trunk are subcircular and are largest and most numerous on the anterior and posterior extremities. Contrary to the situation in most species of this genus, the largest papillae are located ventrally rather than dorsally. Each papilla is characterized by distinctive dark brown platelets which are evenly dispersed around a clear central area. Individual platelets are also scattered over the cuticle among the papillae.

The longitudinal muscle bundles show considerable anastomosis ; immediately anterior to the origin of the retractors they number approximately 20. Four retractor muscles originate at nearly the same level in the middle third of the trunk, although the dorsals are slightly anterior to and somewhat thinner than the ventrals. The dorsal and ventral retractors soon join to form left and right retractors which remain separated for most of their length.

The gut is attached posteriorly by a spindle muscle and is comprised of approximately 25 single coils. A single fixing muscle extends from an attachment to the body wall left of the ventral nerve cord in the mid-region of the body to the intestinal coil. Strong wing muscles attach the rectum to the body wall in the region of the anus. A prominent contractile vessel with numerous villi runs along the oesophagus and continues into the beginning of the intestinal coil.

Part of the left nephridium is missing, but the right nephridium is three-quarters of the length of the trunk and is attached to the body wall for two-thirds of its length.

REMARKS : This specimen is identical to *Phascolosoma antillarum* Grube and Oersted 1859 as evidenced by similarities in the form and distribution of papillae and platelets, tentacular form and pattern, structure of contractile vessel and villi, relative length and attachment of nephridia, the number of longitudinal muscle bundles and the attachment and union of retractor muscles.

Phascolosoma albolineatum Baird, 1868

Phascolosoma albolineatum Baird, 1868, p. 91-92.

Phymosoma albolineatum : Selenka and de Man, 1883, pp. 71-72, pl. ix, fig. 128-129.

HOLOTYPE : Reg. No. 1925.25.1.

TYPE LOCALITY : Philippine Islands. Coll. Cuming.

The holotype is still in fairly good condition and had been dissected previously. It is presumed to be the specimen described and figured by Selenka, de Man and Bülow (1883), since they state that their description is based on Baird's original specimen. They described it fully and the species remains valid.

***Phascolosoma capsiforme* Baird, 1868**

Phascolosoma capsiforme Baird, 1868, p. 83-84, pl. ix, fig. 3 ; Selenka, de Man, and Bülow, 1883, p. 27-28, pl. iv, figs. 38-39.

SYNTYPES : Reg. No. 1842.2.24.60/63.

TYPE LOCALITY : Falkland Islands. Coll. W. Wright.

One of Baird's specimens was examined by Selenka, de Man, and Bülow who gave it a full description, including an account of the internal anatomy and figures of the papillae. Since none of the four syntypes in the Museum had been dissected, it must be presumed that the specimen described by Selenka was not returned or has been lost. The four remaining specimens are in excellent condition. One is partially expanded ; the others are contracted.

The characters, as reported by Selenka (1883), agree with those of *Golfingia margaritacea* Sars, a common species of northern seas and now recorded from a number of localities in the Antarctic. Selenka, de Man, and Bülow noted the close resemblance between the two species, and several authors have since called it a subspecies of the northern species (Fischer 1896, 1913, Benham 1922, Edmonds 1965). In a description of species from the Ross Sea, Edmonds (1965) reviewed previous reports of the northern and southern forms and concluded that the southern species is properly designated as *Golfingia margaritacea capsiformis* (Baird).

***Phascolosoma fasciatum* Baird, 1868**

Phascolosoma fasciatum Baird, 1868, p. 89.

SYNTYPES : Reg. No. 1849.8.4.18/19.

TYPE LOCALITY : Madiera (Azores). Coll. N. Lister.

The two syntypes are in good condition and neither has been dissected previously. Baird (1868) characterized the species by the brown bands on the introvert, the reddish brown spots on the body and the many small reddish papillae of similar size anteriorly and posteriorly. From Baird's description, Selenka, de Man, and Bülow suggest in their Appendix E that *Phascolosoma fasciatum* Baird may be the same as *Phascolosoma granulatum* (Leuckart) 1828.

DESCRIPTION : In both syntypes the introvert is partially retracted ; the trunk of one specimen measures 30 mm in length with a maximum width of 5 mm and that of the other is 20 mm long with a maximum width of approximately 4 mm. The exposed portion of the introverts of the two specimens are marked by dorsal reddish brown bands and pale, inconspicuous papillae, becoming larger and more numerous toward the base of the introvert. In the anal region the papillae are variable in size and shape, the larger ones being pyramidal and the others flat and low. The papillae of the middle trunk are smaller and rounded, whereas those of the posterior trunk are comparable in size and shape to the anal papillae.

The smaller syntype was dissected (by ACS) and an incision was made in the anterior introvert for a study of the hooks and small papillae lying between the hooks. The hooks, measuring approximately 0.072 mm at the base and 0.074 mm high, are

characterized by a well-developed central clear streak which shows no basal expansion and a marked terminal curvature with a secondary tooth (Figure 17).

The longitudinal muscle bundles in the dissected syntype number 22 immediately anterior to the origin of the dorsal retractors and show little anastomosis. A pair of ventral retractor muscles originates in the posterior third of the trunk and a pair of dorsal retractors in the middle third. The roots of the ventrals span muscle bundles 2 to 8 and the dorsals 5 to 8.

A fixing muscle arises left of the ventral nerve cord anterior to the origin of the dorsal retractors and divides into two branches, one attaching to the rectum and one to the first descending intestinal coil.

The nephridia open at the level of the anus and extend posteriorly to the origin of the dorsal retractors. They are attached for approximately a half of their length.

REMARKS : The characters as observed in this examination of the syntypes lend support to Selenka's suggestion that *Phascolosoma fasciatum* Baird 1868 is identical with *Phascolosoma granulatum* (Leuckart) 1828. The internal anatomy is essentially the same as described by Selenka for *P. granulatum* and the small papillae of the introvert (Figure 16) and the hooks (Figure 17) correspond in structure to those figured by Selenka for *P. granulatum* (Selenka, de Man, and Bülow, 1883, Pl. x, Figures 147-149).

Phascolosoma jeffreysii Baird, 1868

Phascolosoma jeffreysii Baird, 1868, p. 88-89.

HOLOTYPE : Reg. No. 1863.12.4.8.

TYPE LOCALITY : Spezzia. Coll. J. G. Jeffreys.

Baird (1868) defined the species on the basis of its shape, the red markings on the dorsal body, transverse striations, density of papillae on posterior and anterior trunk, sparsity of papillae on introvert, and the dorsal reddish brown rings of the introvert. His reasons for distinguishing *Phascolosoma jeffreysii* as a species separate from *P. fasciatum* are not clear. The following description includes internal anatomy and is intended to supplement Baird's report.

DESCRIPTION : The body length of the holotype is 40 mm with approximately 10 mm of the introvert exposed and the remainder retracted. Papillae at the base of the introvert are pyramidal in shape and reddish-brown in colour ; at the posterior extremity many are similar, but others are rounded and colourless. Papillae over the rest of the body are mostly smaller, flat, and colourless. Hooks on the retracted introvert possess an accessory tooth and a clear central streak with little basal expansion (Figure 19). They measure approximately 0.054 mm at their base and 0.049 mm in height.

The holotype was dissected by one of the present authors (ACS). The longitudinal musculature is divided into 20 bundles in the region of the origin of the ventral retractors. The ventral retractors originate in the posterior third of the body ; the root of the left ventral retractor spans bundles 2-6 and the right 2-7. The dorsal

retractor muscles originate more anteriorly in the middle third of the trunk and their roots span bundles 4-7. A fixing muscle with two branches attaches to the rectum and to the first descending coil of the gut. The spindle muscle attaches posteriorly to the body wall and anteriorly it attaches immediately in front of the anus. Two nephridia open at the level of the anus and are attached to the body wall for two-thirds of their length. They extend posteriorly to the origin of the ventral retractor muscles.

REMARKS : This specimen exhibits striking similarities to the syntypes of *Phascolosoma fasciatum* Baird and, like them, to descriptions of *P. granulatum* (Leuckart) in the shape and distribution of papillae, pigment markings on the trunk and introvert, and internal anatomy. The hooks are similar in structure to those of *P. fasciatum* (Figures 19, 17), except that the size and relative proportions vary and the clear area on the concave side is more distinct. Without seeing the specimen Selenka, de Man, and Bülow (1883) suggested that *P. jeffreysii* Baird 1868 might be the same as *P. granulatum* (Leuckart) 1828.

Phascolosoma lordi Baird, 1868

Phascolosoma lordi Baird, 1868, p. 92-93.

HOLOTYPE : Reg. No. 1860.3.21.75.

TYPE LOCALITY : Esquimalt Harbour, Vancouver Island. Coll. J. K. Lord.

Baird (1868) suggested that this specimen, found in the same locality as two specimens which he identified as *P. agassizii*, might be a variety of the latter. He distinguished *P. lordi* as a separate species on the basis of differences in "general appearance, size, and colour". In Appendix E of their monograph, Selenka, de Man, and Bülow (1883) stated that *P. lordi* Baird seemed to be a variety of *P. agassizii* Keferstein. Fisher (1952) in his treatise on "Sipunculid Worms of California and Baja California" gave an exhaustive account of *P. agassizii* and included *P. lordi* in the synonymy.

Internal anatomy of Baird's holotype, not heretofore reported, is similar to *Phascolosoma agassizii*. Longitudinal muscle bundles exhibit a high degree of anastomosis; 20 bundles were counted between the origins of the ventral and dorsal retractor muscles. The ventral and dorsal retractors originate in the posterior third of the trunk, the dorsals slightly anterior to the ventrals, and the muscles on each side soon fuse to form two muscles which continue separately to their union in the anterior introvert. A spindle muscle attaches to the posterior extremity of the trunk and anteriorly it adheres along the length of the rectum, attaching to the body wall immediately anterior to the anus. One fixing muscle is present, but accurate observations of its attachments were precluded by the fragile condition of the gut.

A hook from the anterior introvert of the holotype is illustrated (Figure 18). A comparison with Fisher's (1952) illustrations of hooks of *P. agassizii* shows similarities to most of the latter in the lack of a secondary tooth, the course and relative width of the central clear streak, and the basal triangular clear streak on the convex side.

***Phascolosoma nigriceps* Baird, 1868**

Phascolosoma nigriceps Baird, 1868, p. 90, pl. xi, figs. 1, 1a.

Phymosoma antillarum : Selenka, de Man, and Bülow, 1883, p. 58.

SYNTYPES : Reg. No. 1859.12.7.63 a/b.

TYPE LOCALITY : St. Thomas, West Indies. Coll. Cuming (?).

Baird lists specimens from St. Thomas, Jamaica, and Chile. Two specimens from St. Thomas are now present in the collections at the British Museum as syntypes and neither of these had been dissected. Selenka, de Man, and Bülow report that they examined Baird's original specimen from Chile, and it seems that this was not returned. These authors referred Baird's specimen to *Phascolosoma antillarum* Grube and Oersted 1858.

The two syntypes from St. Thomas, both with retracted introverts, measure 25 mm in length with a maximum width of 7 mm and 45 mm long with a maximum width of 10 mm. Prominent papillae, typically low and flattened with dark brown platelets of similar size, cover the trunk and are largest and most numerous in the anal region. In the larger specimen the posterior papillae are similar to those of the anal region, whereas in the smaller specimen the posterior cuticle is white and thin with only a few small papillae. In both specimens the platelets are scattered over the cuticle among the papillae.

The smaller specimen was dissected (by MER). The longitudinal musculature is divided into anastomosing bundles which number approximately 25 immediately posterior to the origin of the retractor muscles. The 4 retractor muscles originate at nearly the same level at the beginning of the posterior third of the trunk. A fixing muscle attaches on the rectum, anterior to a prominent caecum. The rectum is long and the intestine is comprised of approximately 22 single coils. A well-developed contractile vessel with numerous branched villi extends along the oesophagus into the first intestinal coil. The nephridia are attached to the body wall except for the posterior extremity and reach posteriorly to a level slightly below the origin of the retractor muscles.

The characters reported above correspond to those of *Phascolosoma antillarum* Grube and Oersted 1858 and thus give supporting evidence for Selenka's synonymy of *P. nigriceps* Baird 1868.

***Phascolosoma perlucens* Baird, 1868**

Phascolosoma perlucens Baird, 1868, p. 90-91, pl. x, figs. 2, 2a

Phymosoma varians : Selenka, de Man and Bülow, 1883, p. 70

SYNTYPES : Reg. No. 1847.12.30.11.

TYPE LOCALITY : Jamaica, from holes in coral rocks. Coll. Grosse.

Of the three extant syntypes, one was figured by Baird in two illustrations of the entire animal showing external form and size. Selenka, de Man, and Bülow (1883, p. 70) list *Phascolosoma perlucens* Baird in a synonymy of *Phascolosoma varians*

Keferstein, with the explanatory statement "Die von uns vorgenommene Untersuchung des BAIRD'schen Originalexemplars ergab, dass diese Art mit dem *Ph. varians* KEFERSTEIN identisch ist!". It is improbable that these authors examined any of the extant syntypes of *P. perlucens* since these specimens do not correspond to *P. varians*, but rather to *P. dentigerum* Selenka and de Man (see below). The occasion for the error remains unexplained.

DESCRIPTION : The largest of the three specimens, the one figured by Baird, measures 35 mm in length to the base of the introvert, which is almost entirely retracted, and 3.5 mm in maximum width. In the smallest specimen the trunk is 21 mm long with a maximum width of 1.5 mm and the introvert is partially extended to a length of 7 mm. The trunk of the third specimen is 25 mm in length, 2 mm in maximum width, and the partially extended introvert is 10 mm long. The trunk regions of all specimens are pale and whitish with a thin integument through which longitudinal muscle bundles are visible. The preanal regions and the base of the dorsal introvert are markedly darker due to a concentration of reddish brown, conical, sometimes sharply pointed papillae which become progressively smaller and lighter anteriorly. On the ventral introvert the papillae are generally less prominent. Some papillae on the posterior introvert are pointed in a posterior direction. On the anterior half of the trunk, posterior to the anus, the papillae are colourless, low, mostly oval in shape, and widely spaced. The papillae on the posterior half of the trunk are more conical and light brown in colour, increasing in height and density posteriorly and becoming sharply pointed at the posterior extremity. Platelets surrounding the central opening of the papillae are darker than peripheral platelets. Hooks from the anterior retracted introvert of the largest specimen measure 0.061 mm at the base and 0.065 mm in height (Figure 15). They are sharply bent terminally and show an accessory tooth. The clear triangular area is well-defined.

One of the specimens, intermediate in size, was dissected (by MER). The longitudinal muscle bands show little anastomosis and number 20-22 posterior to the origin of the ventral retractors. The spindle muscle attaches immediately anterior to the anus and is attached to the posterior extremity. There are approximately 16 single intestinal coils. A single fixing muscle originates to the left of the ventral nerve cord, anterior to the roots of the dorsal retractor muscle and gives off a branch to the postoesophageal intestine and one to the rectum. Two nephridia, opening at the level of the anus, extend posteriorly one-half the length of the trunk and attach to the body wall for three quarters of their length. A pair of black eye-spots is present on the brain. Sixteen rows of hooks were counted through the wall of the retracted introvert.

REMARKS : *Phascolosoma perlucens* Baird 1868 corresponds to *Phascolosoma dentigerum* Selenka and de Man 1883. Similarities are apparent in the following taxonomic characters : form, distribution, and colouration of papillae, structure of hooks (Figure 15) and hook papillae (Figure 14), relative proportions of the body, and essential features of internal anatomy.

***Phascolosoma placostegi* Baird, 1868**

Phascolosoma placostegi Baird, 1868, p. 89-90.

HOLOTYPE : Reg. No. 1965.25.11

TYPE LOCALITY : Cape of Good Hope. Coll. Krauss ; found lodged in a mass of Serpulidae (*Placostegus*).

The holotype, hardened and brittle, is in very poor condition and disintegrates when manipulated. None of the internal characters could be distinguished, nor any hooks recovered. The reason for the poor state of preservation is found in Baird's statement that the specimen when found "was dry, but afterwards moistened and put into spirits" (Baird, 1868, p. 90). Since Baird's description was limited to non-specific external characters, the species cannot be defined and the name *Phascolosoma placostegi* therefore must be considered as a nomen dubium.

***Phascolosoma planispinosum* Baird, 1868**

Phascolosoma planispinosum Baird, 1868, p. 93.

Phymosoma nigrescens : Selenka, de Man, and Bülow, 1883, p. 73.

HOLOTYPE : Reg. No. 1965.25.6.

TYPE LOCALITY : Unknown. Coll. Cuming.

The holotype has been allowed to dry out completely at some time and is quite contracted and inflexible. It had been dissected previously and most of the internal organs are missing in part or entirely. Fortunately the specimen was seen by Selenka, de Man and Bülow (1883) who placed it in synonymy with *Phascolosoma nigrescens* Keferstein 1865 and considered it to be identical with a variety from the Philippine Islands which they described but to which they did not give a varietal name. Since Baird stated that he had only one specimen, this is undoubtedly the same specimen which Selenka examined.

In spite of the poor condition of the specimen, it was possible to recover some hooks, one of which is figured (Figure 20). This hook differs from those of specimens of *Phascolosoma nigrescens* from the Fiji Islands and Mauritius illustrated by Selenka (Selenka, de Man, and Bülow 1883, Figures 130, 135), in that the clear streak of *P. planispinosum* is quite distinct from the clear triangular area and an accessory tooth is lacking. There is, however, a thickening in the basal plate, similar to that characteristic of *P. nigrescens* (Fisher 1952). The triangular space was not as distinct in all of the hooks examined as in the one illustrated (Figure 20), but the form of the central clear streak appeared consistent. Selenka, de Man and Bülow did not illustrate hooks from the specimens of *P. nigrescens* from the Philippines with which they considered *P. planispinosum* identical.

Themiste lageniformis Baird, 1868

Themiste lageniformis Baird, 1868, pp. 98-99, pl. 10, figs. 3-3c.

SYNTYPES : 1965.25.9/10

TYPE LOCALITY : Australia?

The two specimens on which Baird based his original description of the species are in the same condition as he indicated at that time. In one specimen the introvert and tentacles are extended, but the animal is hard and brittle, apparently having been desiccated at some time after preservation. In the second specimen the introvert is completely retracted. The second specimen was dissected by one of the present authors (ACS).

Baird noted the resemblance of the shape of the extended body to a flask and from this character he derived the specific name, *lageniformis*, meaning flask-shaped. Other characters used by Baird to define the species were as follows : striations and folds of the skin approaching a clathrate pattern posteriorly ; a long, cylindrical introvert covered by a wrinkled, plicate skin ; six pinnate tentacles (the number 6 was followed by a question mark).

The following description includes information on the internal anatomy of one of the syntypes and is intended to supplement Baird's reported observations.

DESCRIPTION : The extended specimen, previously desiccated and grotesquely contracted in the mid-region of the trunk, measures approximately 22 mm in length to the base of the tentacles. The number of tentacles appears to be six, but the specimen was preserved in such a way that the oral disc was not visible and manipulation was precluded by the brittle condition ; hence, it was not possible to affirm whether these were six primary stems. Hooks do not occur on the introvert. The anal opening occurs along the narrowed anterior portion of the body, 8 mm from the base of the tentacles, and the introvert is approximately one-third to one quarter the length of the remainder of the body, an exact figure being difficult to ascertain because of the contracted region in the middle of the body.

In the other syntype, in which the anterior end is retracted, the length of the trunk from anus to posterior extremity is approximately 24 mm and the withdrawn introvert is about a quarter of this length. Longitudinal and transverse grooves in the skin form a tessellated pattern over most of the trunk. The pattern is most pronounced at the base of the introvert and posterior extremity where the grooves are deepest. In the middle of the body the longitudinal grooves are weak or non-existent and the transverse grooves shallow ; consequently, the tessellation is not so apparent. The openings of the epidermal glands occur within the rectangles of the tessellation ; in the middle of the body where the skin is more distended they are most readily observed and appear as openings in the centre of concave depressions (Figure 13).

Internally the body wall musculature of the dissected syntype is smooth, two thick retractors originate in the posterior fifth of the trunk remaining separate for most of their length, and the gonad appears as a thin strand on the base of the retractors (Figure 12). The oesophagus is directed posteriorly to a point at the base of the ventral retractors where it is attached by a fixing muscle ; it then turns

abruptly anteriorly to enter the intestinal coil. The intestine is comprised of approximately 28 single coils and has no posterior attachment. Through the thin walls of the descending gut the contents can be seen to consist of fine sand or mud particles which have been compacted and twisted into a spiral form. A caecum is present at the beginning of the rectum. The spindle muscle, passing by and attaching to the base of the caecum, runs along the dorsal side of the rectum and appears to insert on it. There is no attachment of the spindle muscle to the posterior body wall. Prominent wing muscles fasten the rectum to the body wall in the region of the anus.

There are three fixing muscles. F_1 attaches the oesophagus to the body wall just posteriorly to the inner margin of the left retractor muscle. Broken from its site of origin on the body wall, F_2 is attached to the first descending intestinal coil. F_3 , attached to the body wall near the dorsal midline in the anterior third of the body, proceeds beneath the intestinal coil to attach to the beginning of the rectum as it emerges from the intestinal coil.

A prominent contractile vessel is adjoined to the descending oesophagus but ends just beyond the point at which the oesophagus curves anteriorly toward the intestinal coil. Anteriorly the vessel is very much enlarged and distended with cellular elements, but more posteriorly it gives off numerous tufts of short filiform villi which frequently bifurcate near their basal attachments.

Two nephridia hang freely in the body cavity. The nephridiopores open at about the same level as the anus.

REMARKS : These specimens correspond to Selenka's (1883) description and illustrations of *Dendrostoma signifer* in the characteristic arrangement and form of the contractile vessel and villi, the number and attachment of the fixing muscles, the relatively short introvert, and the furrowing of the skin. Although Selenka does not mention a caecum for *D. signifer*, other authors (Edmonds 1956, Ikeda 1904, Wesenberg-Lund 1959) have reported a rectal diverticulum for this species. The number of tentacular stems has been variously reported as 5 or 6 (Selenka 1883) or as 4 (Ikeda 1904, Edmonds 1956, Fischer 1919).

Although Selenka lists *Themiste lageniformis* in an appendix (Selenka, de Man, and Bülow, 1883, Appendix E), he makes no mention of the name elsewhere in the monograph. Presumably he had not examined Baird's syntypes when he described *Dendrostoma signifer* as a new species.

Aspidosiphon cumingii Baird, 1868

Aspidosiphon cumingii Baird, 1868, p. 102, pl. xi, fig. 2 ; Selenka, de Man and Bülow, 1883, p. 113-115.

TYPE LOCALITY : Philippine Islands. Coll. Cuming.

Baird's description was superficial, but the holotype was fully described by Selenka, de Man and Bülow and the name remains valid. The specimen is missing from the collection, possibly never returned to the British Museum (Natural History) by Selenka.

Aspidosiphon jukesii Baird, 1873

Aspidosiphon jukesii Baird, 1873, p. 97.

HOLOTYPE : Reg. No. 1965.25.3.

TYPE LOCALITY : Lee Sandbanks (Great Barrier Reef, Australia?).

Baird's brief description (Baird, 1873) enumerated a few general external features, but provided no significant characters by which this species could be distinguished by other authors. Hence the species was not recognized in the literature, even though the type remained extant in reasonably good condition in the collections of the British Museum (Natural History). The holotype was dissected by one of the present authors (ACS) and a report of its internal anatomy is presented here. The specimen had been removed at the time of its collection from a solitary coral, the remains of which are still preserved.

DESCRIPTION : Preserved in a curved, U-shaped position, the specimen measures 25 mm along the median line of the outer, dorsal curvature with a maximum width of approximately 5 mm (Figure 24). The introvert is entirely retracted. The integument of the posterior two-thirds of the trunk is thin, distended, and pale yellow, whereas the anterior one-third is more tightly contracted and a deeper yellow. A well-developed, dorsally oblique anal shield is clearly set off from the remainder of the body (Figure 21, 22). Approximately 12 major longitudinal furrows, not all complete, mark the flattened surface of the shield which is composed of large, irregularly shaped, amber-coloured platelets. Lateral and ventral extensions of the shield are distinguished by raised papillae, densely packed, with embedded amber platelets similar to those of the dorsal surface of the shield. A small clear spot marks the apex of each papilla. Over the remainder of the trunk the papillae are more widely dispersed, smaller, and flatter with a relatively large central area surrounded by one or more rings of pale yellow coalesced platelets which form clumps of varying sizes (Figures 28, 29). The papillae may reach a width of 0.7 mm in the posterior quarter of the trunk, but they are only slightly elevated from the surface with a maximum height of approximately 0.3 mm. The posterior shield is circular, well-demarcated, but lighter in color than the anal shield (Figure 23). There are a few weak, irregular radial striations which do not extend to the center of the shield. The constituent pale yellow platelets vary in size and are larger and darker in the central portion.

Small, pale hooks are arranged in rows on the anterior introvert. At their base the hooks measure about 0.028 mm and their height is 0.025 mm. The hooks are weakly curved with a secondary terminal point and a large central clear area which is widened proximally to include the entire base (Figure 25). Introvert papillae, measuring about 0.013 mm in height and 0.008 mm in diameter, are dispersed among the rows of hooks (Figure 27). Larger spines with a height of 0.035 mm are scattered more posteriorly over the introvert. Because of its retracted condition, the entire introvert was not examined.

The musculature of the body wall is smooth. Two retractors attach at the posterior extremity in the region of the terminal shield. Separated posteriorly, they soon join and are united for about two-thirds of their total length. At the point of union

of the retractors the oesophagus bends in an anterior direction to join the intestinal coil. Numerous coils (approximately 30 single coils) comprise the intestinal spiral, but an accurate count is not possible because of the poor state of preservation of the gut. A spindle muscle attaches the intestine posteriorly. The anal opening is immediately posterior to the flattened anterior shield and the two nephridia open at nearly the same level. The nephridia are partially attached to the body wall, but unfortunately the free ends have been broken off so that neither the length of the nephridia nor the relative extent of their attached portion can be determined.

REMARKS : This specimen resembles *Aspidosiphon corallicola* Sluiter, 1902, both in its habitat in a solitary coral and in the following taxonomic characters : origin and union of the two retractor muscles, morphology of anterior and posterior shields, and the structure and distribution of the hooks, spines, and papillae.

Although similar in basic structure, the hooks and spines differ in size for the holotype of *Aspidosiphon jukesii* and *A. corallicola*. The height of the hooks is the same in both (0.025 mm), but the width in *A. corallicola* is proportionately greater. Moreover, Sluiter (1902) reported that in *A. corallicola* the spines were smaller than the hooks, whereas the reverse is true for the holotype of *A. jukesii*. Without additional measurements to indicate the range of variation within and among individuals the significance of the size discrepancies is difficult to evaluate. However, the other important similarities between *A. jukesii* and *A. corallicola* suggest that the two names represent a single species. *A. jukesii* has priority, since it is the older name.

Pseudasipidosiphon gracile Baird, 1868

Pseudasipidosiphon gracile Baird, 1868, p. 103, pl. x, fig. 1, 1a.

Aspidosiphon gracilis : Selenka, de Man and Bülow, 1883, p. 122-123, pl. ii, fig. 22, pl. xiv, fig. 209-213.

SYNTYPES : Reg. No. 43.5.15.58a/b.

TYPE LOCALITY : Philippine Islands. Coll. Cuming.

Baird seems to have had three specimens, one of which was examined and described by Selenka. Since neither of the two specimens in the collection has been previously dissected, it is probable that Selenka did not return the specimen which he described. Selenka gave a complete, well-illustrated description of Baird's specimen, so that the specific name remains valid.

Echiurus farcimen Baird, 1873

Echiurus farcimen Baird, 1873, p. 97.

Echiurus chilensis : Shipley, 1899, p. 342.

HOLOTYPE : Reg. No. 69.6.28.18.

TYPE LOCALITY : Punta Arenas, Patagonia. Coll. Cunningham.

In Baird's brief description of the species, he mentioned 5 specimens, the largest of which was 16 inches in length. Only one of these specimens remains in the collection and, although previously dissected, it is still in good condition. Its approximate measurements are 170 mm in length and 125 mm in maximum circumference. With

rounded extremities and considerably reduced prostomium, the specimen resembles a sausage in shape. One of the members of the anteroventral pair of setae is missing, but the intact seta, slightly curved, is extended to a length of 4 mm. A single ring of 12 smaller setae, marked by a mid-ventral gap, encircles the posterior extremity. There are three pairs of prominent nephridia, each with two long, spirally coiled lips. Two anal vesicles reach lengths approximately one-half that of the body.

Shipley (1899) considered Baird's specimens of *Echiurus farcimen* to be synonymous with *E. chilensis* Max Müller 1852 and later authors (Fisher 1946, Wesenberg-Lund 1955, Amor 1965) have accepted this synonymy. Since 1907, when Seitz revised the genus, this species has been known as *Urechis chilensis*.¹

TABLE I

1. Gray and Baird species-names which are senior subjective synonyms of currently accepted names.

Senior synonym	Current name
<i>Siphunculus arcuatus</i> Gray, 1828	<i>Phascolosoma lurco</i> (Selenka & de Man, 1883)
<i>Phascolosoma perlucens</i> Baird, 1868	<i>Phascolosoma dentigerum</i> (Selenka & de Man, 1883)
<i>Themiste lageniformis</i> Baird, 1868	<i>Themiste signifer</i> (Selenka & de Man, 1883)
<i>Aspidosiphon jukesii</i> Baird, 1873	<i>Aspidosiphon corallicola</i> Sluiter, 1902

2. Gray and Baird species-names which are currently accepted.

Themiste hennahi Gray, 1828
Sipunculus angasi Baird, 1868
Phascolosoma albolineatum Baird, 1868
Aspidosiphon cumingi Baird, 1868
Aspidosiphon gracile (Baird, 1868)

3. Gray and Baird species-names which are junior subjective synonyms of currently accepted names.

Junior synonym	Current name
<i>Siphunculus dentalii</i> Gray, 1828	<i>Phascolion strombi</i> (Montagu, 1804)
<i>Siphunculus tuberculatus</i> Gray, 1828	<i>Phascolosoma noduliferum</i> Stimpson, 1855
<i>Sipunculus aeneus</i> Baird, 1868	<i>Siphonosoma australe</i> (Keferstein, 1865)
<i>Sipunculus deformis</i> Baird, 1868	<i>Siphonosoma cumanense</i> (Keferstein, 1866)
<i>Sipunculus eximioclathratus</i> Baird, 1868	<i>Sipunculus nudus</i> Linnaeus, 1766
<i>Phascolosoma aethiops</i> Baird, 1868	<i>Phascolosoma antillarum</i> Grube & Osted, 1859

1. Seitz (1907) erected the genus *Urechis* for the species *Echiurus chilensis* Max Müller and *E. uncinatus* von Drasch. Riveras Zúñiga (1942), on grounds of priority, revived the generic name *Pinuca* Hupé in Gay 1854, but more recently Jones, Hedgpeth, and Hand (1968) have applied to the International Commission on Zoological Nomenclature for the suppression of *Pinuca*. At this date no action has been taken on this request.

Junior synonym	Current name
<i>Phascolosoma capsiforme</i> Baird, 1868	<i>Golfingia margaritacea</i> (Sars, 1851)
<i>Phascolosoma fasciatum</i> Baird, 1868	<i>Phascolosoma granulatum</i> (F. S. Leuckart, 1828)
<i>Phascolosoma grayi</i> Baird, 1868 (nom. nov. pro. <i>Siphunculus tuberculatus</i> Gray, 1828)	<i>Phascolosoma noduliferum</i> Stimpson, 1855
<i>Phascolosoma jeffreysii</i> Baird, 1868	<i>Phascolosoma granulatum</i> (F. S. Leuckart, 1828)
<i>Phascolosoma lordi</i> Baird, 1868	<i>Phascolosoma agassizii</i> Keferstein, 1866
<i>Phascolosoma nigriceps</i> Baird, 1868	<i>Phascolosoma antillarum</i> Grube & Oersted, 1859
<i>Phascolosoma planispinosum</i> Baird, 1868	<i>Phascolosoma nigrescens</i> Keferstein, 1865
<i>Echiurus farcimen</i> Baird, 1868	<i>Urechis chilensis</i> Max Müller, 1852

4. Baird name which is a nomen dubium.

Phascolosoma placostegi Baird, 1868.

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MARY E. RICE, Ph.D.,
Associate Curator, Division of Worms,
NATIONAL MUSEUM OF NATURAL HISTORY,
SMITHSONIAN INSTITUTION,
WASHINGTON,
D.C. 20560,
UNITED STATES OF AMERICA.

† Dr A. C. STEPHEN, D.Sc., F.R.S.E.,
Keeper of Natural History,
ROYAL SCOTTISH MUSEUM,
CHAMBERS STREET,
EDINBURGH, 1,
SCOTLAND.

† Obituary : Waterston, A. R. 1966, *Nature*, **211** : 21.

PLATE I

Siphunculus arcuatus Gray. Holotype.
Current Name : *Phascolosoma arcuatum* (Gray)

FIG. 1. Dissected specimen showing internal anatomy. In the preserved specimen the retracted introvert is coiled within the body cavity ; for clarity in the drawing it is straightened and the intestinal coil is pulled aside to reveal other internal structures. AR, anterior retractor ; E, œsophagus ; G, gonad ; I, retracted introvert ; N, nephridium ; NC, ventral nerve cord ; PR, posterior retractor ; R, rectum ; S, spindle muscle ; W, wing muscle. Approximate length of specimen is 100 mm.

FIG. 2. Papilla from middle region of trunk. Note polygonal platelets, smaller and more concentrated around centre, but otherwise evenly distributed. Diameter 0.3 mm.

FIG. 3. Lateral view of holotype, showing external features. Introvert is retracted. A, anus ; NP, nephridiopore. Rectangles a, b, and c, each measuring 1 × 4 mm on specimen, are enlarged at left to show relative size, form and distribution of papillae. 3a. Enlargement of skin area at base of introvert. 3b. Enlargement of skin area from middle region of trunk. 3c. Enlargement of skin area from posterior extremity.

FIG. 4. Diagrammatic representation of body wall from middle third of trunk, showing the coelomic sacs and their relation to the musculature of the body wall and overlying integument. The integument, shown only in the lower right portion of the diagram, is markedly thinner in the areas covering the sacs. CM, circular muscle bundle ; CS, coelomic sac ; IN, integument ; LM, longitudinal muscle bundle ; P, papilla.

FIG. 5. Hook from introvert. 0.08 × 0.07 mm.

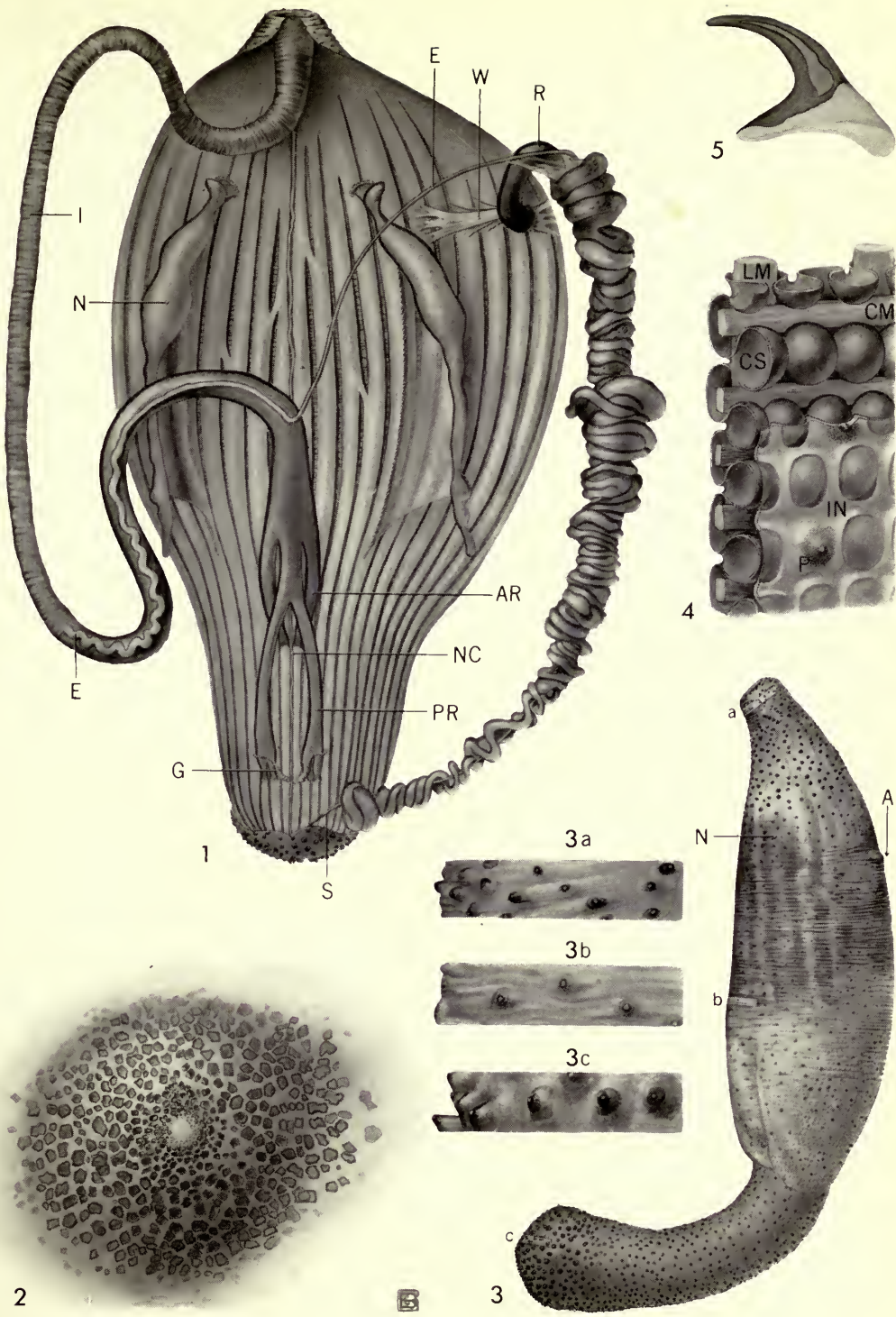


PLATE 2

FIG. 6. *Themiste hennahi* Gray. Paralectotype, dissected specimen. A, anus ; C, caecum ; CV, villi of contractile vessel ; E, oesophagus (looped under right retractor) ; F1, fixing muscle 1 ; F2, fixing muscle 2 (broken) ; F3, fixing muscle 3 ; N, nephridium ; NC, nerve cord ; RM, retractor muscle ; S, spindle muscle. Approximate length of trunk is 37 mm.

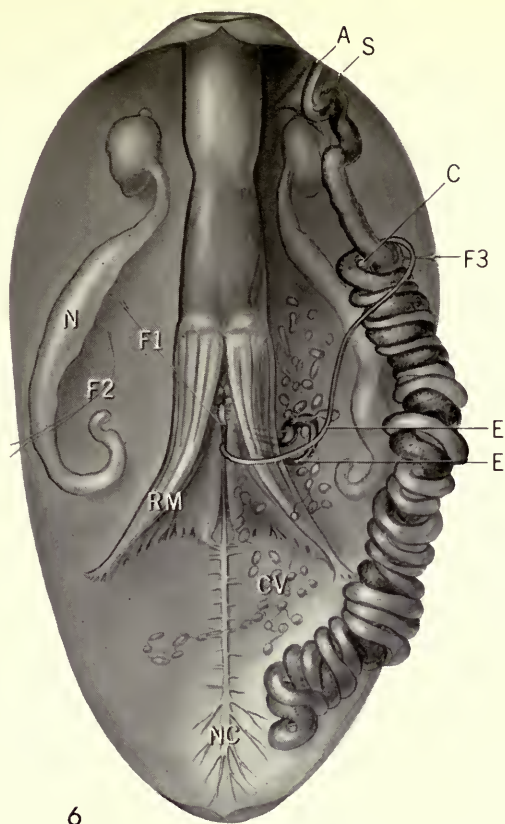
FIG. 7. *Themiste hennahi* Gray. Lectotype. Oral view of tentacular crown, oriented with dorsal tentacles toward bottom of page. The 6 lips surrounding the mouth are evident between the bases of the tentacles.

FIG. 8. *Themiste hennahi* Gray. Lectotype. Lateral view showing external features. A, anus ; NP, nephridiopore. Approximate length of body (minus tentacles) is 70 mm. Squares a, b, c, d, each 1 mm² on specimen, are enlarged on right to show details of skin and papillae. 8a, Introvert. Cuticle has been detached exposing canals of epidermal papillae. 8b, Enlargement of integument in anal region. 8c, Enlargement of integument in middle of trunk. 8d, Enlargement of integument in posterior extremity of trunk.

FIG. 9. *Siphunculus tuberculatus* Gray. Holotype. Current name : *Phascolosoma noduliferum* Stimpson. Hook from introvert. 0.058 mm × 0.047 mm.

FIG. 10. *Siphunculus tuberculatus* Gray. Holotype. Papilla from base of introvert. Diameter, 0.27 mm. Darkly pigmented platelets are arranged in a distinctive ring around the clear central area.

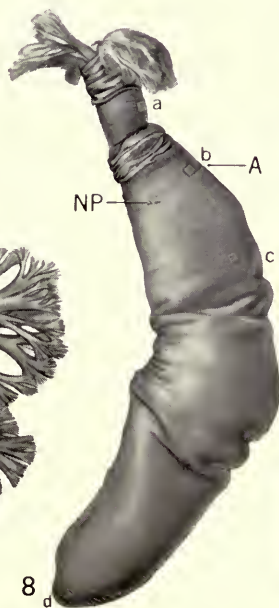
FIG. 11. *Siphunculus tuberculatus* Gray. Holotype. Posterior 1/10 of trunk, showing dense concentration of prominent, dome-shaped papillae.



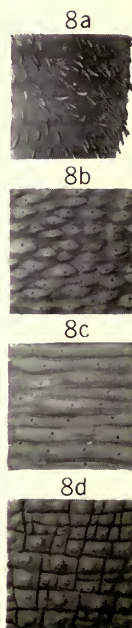
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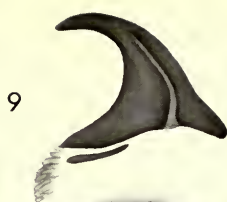


8a

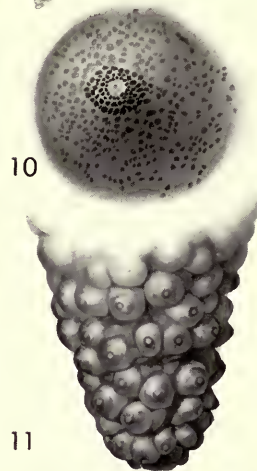
8b

8c

8d



9



10

11

PLATE 3

FIG. 12. *Themiste lageniformis* Baird. Syntype. Dissected specimen. In the specimen the incision had been made through the outer edge of the base of the left retractor muscle, but for purposes of clarity and orientation in the drawing the line of incision and the muscle are reconstructed so that the muscle appears intact. C, caecum ; CV, contractile vessel ; E, oesophagus ; F₁, fixing muscle 1 ; F₂, fixing muscle 2 (broken) ; F₃, fixing muscle 3 ; G, gonad ; N, nephridium ; NC, nerve cord ; R, rectum ; RM, retractor muscle. Approximate length of trunk is 24 mm.

FIG. 13. *Themiste lageniformis* Baird. Syntype. Enlargement of skin (1 mm²) from posterior area of trunk showing horizontal grooves and less distinct vertical grooves surrounding openings of epidermal glands.

FIG. 14. *Phascolosoma perlucens* Baird. Syntype. Apical view of small papilla from introvert, located among rows of hooks on anterior introvert.

FIG. 15. *Phascolosoma perlucens* Baird. Syntype. Hook from anterior introvert. 0.061 × 0.065 mm.

FIG. 16. *Phascolosoma fasciatum* Baird. Syntype. Current name : *P. granulatum* (Leuckart). Lateral view of small papilla from introvert ; situated among rows of hooks on anterior introvert.

FIG. 17. *Phascolosoma fasciatum* Baird. Syntype. Current name : *P. granulatum* (Leuckart). Hook from introvert. 0.072 mm (base) × 0.074 mm (height).

FIG. 18. *Phascolosoma lordi* Baird. Holotype. Current Name : *P. agassizii* Keferstein. Hook from introvert. 0.057 × 0.068 mm.

FIG. 19. *Phascolosoma jeffreysii* Baird. Holotype. Current name : *P. granulatum* (Leuckart). Hook from introvert. 0.057 × 0.049 mm.

FIG. 20. *Phascolosoma planispinosum* Baird. Holotype. Current Name : *P. nigrescens* Keferstein. Hook from introvert. 0.053 × 0.041 mm.

FIG. 21. *Aspidosiphon jukesii* Baird. Holotype. Laterodorsal view of anterior shield. A, anus.

FIG. 22. *Aspidosiphon jukesii* Baird. Holotype. Lateral view of anterior shield. A, anus.

FIG. 23. *Aspidosiphon jukesii* Baird. Holotype. Apical view of posterior shield.

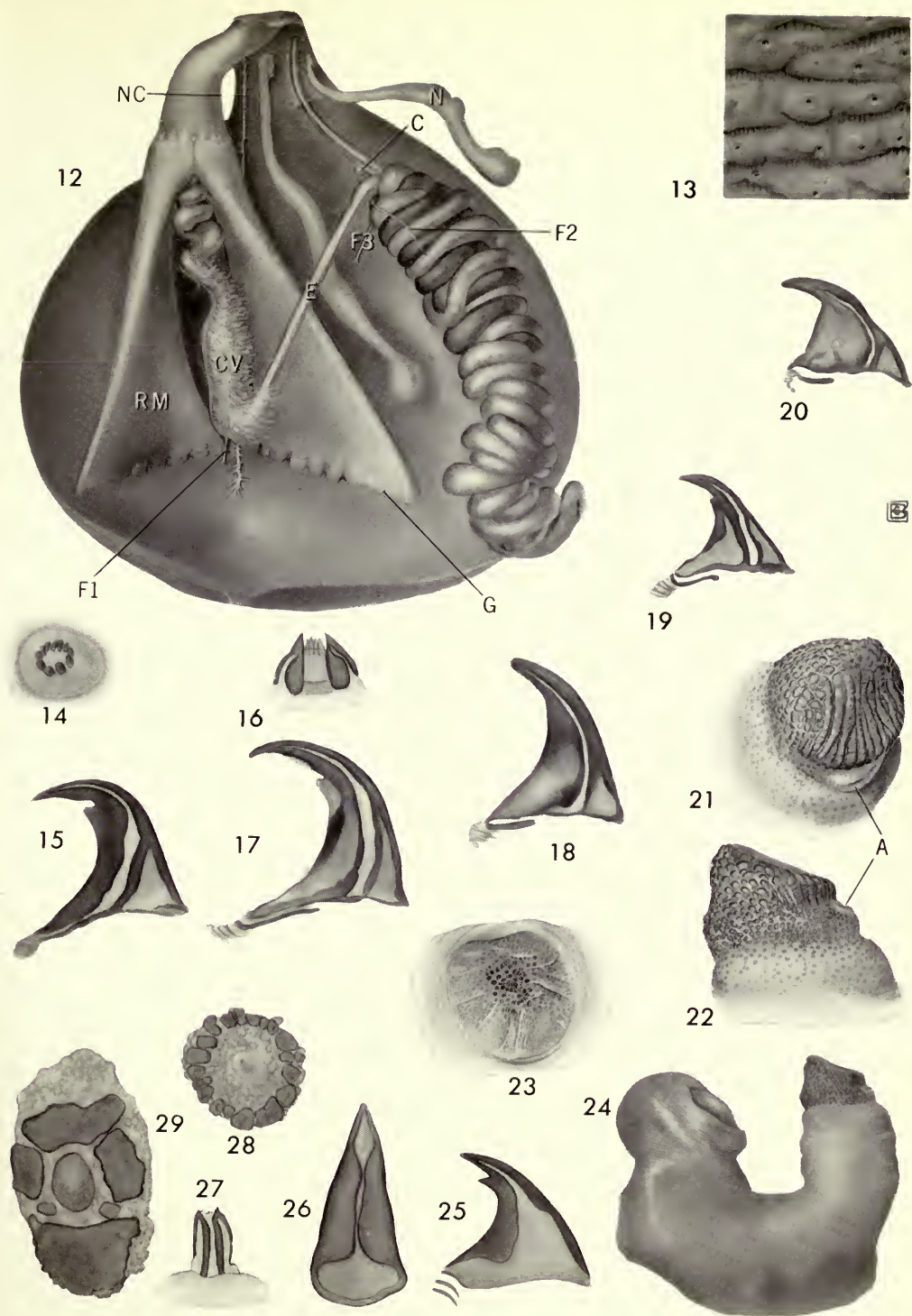
FIG. 24. *Aspidosiphon jukesii* Baird. Holotype. Lateral view of entire animal. Specimen is approximately 25 mm in length, measured along median dorsal curvature.

FIG. 25. *Aspidosiphon jukesii* Baird. Holotype. Hook from anterior introvert. 0.028 (base) × 0.025 mm (height).

FIG. 26. *Aspidosiphon jukesii* Baird. Holotype. Spine from posterior introvert. 0.035 mm (height).

FIG. 27. *Aspidosiphon jukesii* Baird. Holotype. Lateral view of small papilla from introvert ; situated among rows of hooks on anterior introvert.

FIGS. 28, 29. *Aspidosiphon jukesii* Baird. Papillae from the middle region of the trunk showing coalescence of platelets. 28. 0.54 mm, diameter. 29. 0.81 × 0.54 mm.



Printed in Great Britain by
Alden & Mowbray Ltd
at the Alden Press, Oxford

577.2.

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HISTORY)



R. I. JOHNSON

BULLETIN OF
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ZOOLOGY

Vol. 20 No. 3

LONDON : 1971

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BY

RICHARD IRWIN JOHNSON

Museum of Comparative Zoology, Harvard University

Pp. 73-108 ; 2 Plates

BULLETIN OF
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TRUSTEES OF
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By RICHARD I. JOHNSON

INTRODUCTION

AMONG the more important collections of Unionacea in the British Museum (Nat. Hist.) is that of Hugh Cuming, which was acquired in 1866. Cuming sought to have a pair of each described species, and he exchanged shells with most of his contemporaries. Many of his examples of North American species were from J. G. Anthony, whose collection is in the Museum of Comparative Zoology. These specimens often have generalized locality data, which, with the names, were written on the shells by Anthony.

Many of Cuming's shells, and those from the collections of S. Hanley, T. L. Taylor and the Sowerby family, are figured by Lovell Reeve and George B. Sowerby in their uncritical monographs on the Unionacea in the *Conchologia Iconica* between the years 1864-1870. These authors generally figured shells under the names which appeared on the labels before them. Unnamed ones were apparently described as new species. References to the original descriptions are often scanty or missing, and locality data, when present, usually general. Nevertheless, because of the quality of the hand coloured lithograph plates of the various species in natural size, the work has been often referred to by subsequent authors.

The types of Reeve and Sowerby are assumed to have been in the British Museum (Nat. Hist.) if they were based on shells from the collections of Cuming, Hanley or Taylor, though many of these are now missing. The entire Cuming collection was acquired by the museum shortly after his death, but only parts of the collections of Hanley and Taylor were added toward the end of the nineteenth century, after they had passed through the hands of shell dealers. Nevertheless, references to all of the species described from these collections are included in this list if they were described in the *Conchologia Iconica*. None of the species described by Sowerby in this work from the Sowerby family collection were found in the museum. The Sowerbys were shell dealers and it is assumed that these types were sold to various collectors, and therefore, as they were never in the British Museum (Nat. Hist.), they are not included here.

The molluscs described by Alcide D. d'Orbigny in his *Voyage dans l'Amérique Méridionale* during the years 1826-33, were purchased by the museum and enumerated by J. E. Gray in 1854.¹ In most instances Orbigny marked his figured types

¹ Gray, John Edward, 1854, List of the Shells of South America in the Collection of the British Museum. Collected and described by M. Alcide d'Orbigny, "In the Voyage dans l'Amérique Méridionale." London: Published by Order of the Trustees. Pp. 89, 16 mo. (Unionidae, pp. 74-79, nos. 660-700).

with an "x". The names of all of the Unionacea described by Orbigny from his collection of this voyage are included, including those for which no types were found.

The shells of Orbigny have always been kept separate from the main collection. The specimens were originally glued on cards, but when I examined them, many were detached and mixed; however, it was possible to sort them. The shells were cleaned, registered and put in boxes with their original labels.

Many of Arthur Morelet's types were purchased in 1892, shortly after his death, from the shell dealer Hugh Fulton. Also purchased were those species described from the Morelet collection by Fischer and Crosse in their *Mission Scientifique au Mexique et dans l'Amerique Centrale* (Unionacea, 1894). Only those species for which types were found in the museum are included here.

While the collections mentioned above contain the majority of types that can be discussed here, there are many types from various individuals that can be found only by reference to the following list. The general collection of Unionacea had been hastily moved during the Second World War, and many of the shells were detached from the cards on which they had been glued and were badly mixed. Fortunately many of the Hanley, Taylor and Morelet shells were in glass topped boxes. Originally most of the lots consisted of two specimens, often accompanied with scanty data. I was unable to rearrange the general collection, but each lot was examined, and every specimen that gave any evidence that it might be a type, or could have been one that was ever figured in the *Conchologia Iconica* or any other work, was checked against original references, and those which proved to be authentic were placed in a special cabinet which was made available for that purpose.

In addition to the list of types, this paper includes references to several works containing figures of specimens which are not types

ACKNOWLEDGEMENTS

I am grateful to Dr. Norman Tebble who invited me to make the present study, which was done in 1963. He kindly permitted me to remove the types and figured specimens from the general collection, and provided a separate cabinet to house them. He was most kind in assisting me with my many queries, as was Mr. Peter Dance. Miss Joan Rosling painstakingly catalogued and individually numbered all of the shells which were previously unregistered. Mr. Fred Woodward helped me locate some of the figured specimens from the Cuming collection. Thanks are also extended to my colleagues Drs. Kenneth J. Boss and Ruth D. Turner who critically read the manuscript.

Special thanks are extended to Mr. John F. Peake for his part in helping to shepherd this paper through the press, for reading it with special care, and offering critical suggestions.

Part 1

A LIST OF THE TYPES OF RECENT UNIONACEA IN THE BRITISH MUSEUM (NATURAL HISTORY) WITH THEIR ORIGINAL REFERENCES AND TYPE LOCALITIES

The following list is arranged alphabetically by species, giving the author, year and place of publication of the original description, the type locality and collector or

collection when relevant, and includes references to those species which are believed to have been in the museum but are now lost. The word "lost" is in brackets indicating this to be my opinion after a careful search had been made.

The location of the holotype is given when known, even if not in the British Museum (Nat. Hist). If the location of the holotype is unknown, types are listed as syntypes or paratypes, generally the latter if the species was originally figured and there seems to be a possibility that that specimen may be extant. Obviously the use of either of these terms when the location of the holotype is not definitely known is arbitrary.

The selection of a single specimen, or holotype, to represent each described taxon, which is now prevalent, was not necessarily the intent of earlier authors. Nevertheless, the rules promulgated by the XV International Congress of Zoology and published as the International Code of Zoological Nomenclature (1961 and slightly modified in 1964) must be uniformly applied to all taxa.

Article 73 (a) states : If a new nominal species is based on a single specimen, that specimen is the "holotype".

Clearly covered by this article are most of the Unionacea described and figured by Reeve and Sowerby in the *Conchologia Iconica*, since the type lot usually consisted only of the figured specimen. There is usually no evidence in the descriptions that they saw any but the figured specimens. Isaac Lea often mentioned the number of specimens that Cuming sent to him, sometimes a single individual. Yet, some lots of specimens were found in the collection which might pass for types, except that the species was based on the single specimen sent to Lea which is now in the United States National Museum. Some "type" lots contained specimens in excess of the number which were mentioned as having been seen by the describer. The authenticity of paratypes cannot always be ascertained, even in a work such as the present one, but if the holotype has been located their authenticity is less germane.

Article 73 (b) states : If an author states in the description of a new nominal species that one specimen and only one is "the type" or uses some equivalent expression, that specimen is the holotype.

The key to the sensible application of the concept of a single specimen as the holotype to taxa described from 1756 until this concept was firmly established depends on the spirit in which the phrase "equivalent expression" is interpreted. The semantics of this seemingly ambiguous phrase can be argued, but among the definitions of these words are the following : "equivalent"—alike in significance ; "expression"—act or process of representing or making manifest, especially by language.

It was surely not the intent of the Congress to have included this phrase to obfuscate the recognition of holotypes. Rather, it appears to be a clear mandate to use Occam's razor (entities are not to be multiplied without necessity) in their recognition with taxa published before 1961. Thus if a taxon was described with a single set of measurements and not figured, the measured specimen is regarded here, as the holotype. Similarly, if a taxon is described and a single specimen is figured, that specimen is regarded as the holotype. If the measured type cannot be located, a lectotype should be chosen and figured. If the figured type is lost, the selection of a

lectotype can be made, but it may be redundant to do so if the species is readily recognizable from the figure.

Article 73 (c) states : If a new nominal species has no holotype under the provisions of (a) and (b) all of the specimens of the type series are "syntypes", of equal value in nomenclature.

Recommendation 74B suggests : A zoologist should choose as lectotype a syntype of which a figure has been published, if such exists.

This recommendation can be easily complied with if the author figured more than one specimen that can be located. Occasionally, a subsequent author has figured a type, sometimes without design, in the case of previously unfigured species, which can be selected.

It is further recommended (74D) : When possible a lectotype should be chosen from syntypes in the collection of a public institution, preferably of the institution containing the largest number of syntypes of the species, or containing the collection upon which the author of the nominal species worked, or containing the majority of his types.

Recommendation 74D presents both ethical and practical problems, but if Article 73 (b) is interpreted as suggested above, as it is in this paper, these problems are minimal.

The references to Isaac Lea's *Observations on the Genus Unio* do not include plates and figures, since they are always the same as the preceding reference. Only the pages were renumbered in this reprint.

All locality data, contained in brackets, are additions to already published records and are from original labels or modern atlases.

The following abbreviations have been used in this list :

ANSP Academy of Natural Sciences of Philadelphia, Pennsylvania.

BMNH British Museum (Nat. Hist.). London.

MCZ Museum of Comparative Zoology, Cambridge, Massachusetts.

USNM United States National Museum, Washington, D.C.

abdalliana Bloomer, *Caelatura aegyptiaca* : 1946, Proc. Mal. Soc. London, **27** : 70, pl. 6, figs. 4-5 (Hag Abdalla, north of Sennaar, Soudan). Paratype BMNH 1948.5.5.6.

abnormis Morelet, *Unio* : 1862, Rev. et Mag. de Zool. (2) **14** : 480 (Bangkok [Thailand]) ; 1875, Séries Conch., pt. 4, p. 347 [not fig.]. Syntype BMNH 93.2.4.1374.

acorrhynchus Martens, *Unio* : 1895, Sitzber. Gesell. Natur. Freunde, Berlin, p. 214 (Fluss Naemingang bei Hatanggyöng [südlich von Keumsan, Prov. Chöllado] und in einem Zufluss des Imjingang [6 km. von Inchön, Prov. Kangwondo] Korea) ; Martens 1905, Zool. Jahrb., Suppl. 8, p. 61, pl. 3, fig. 4. Paratype BMNH 94.11.24.11.

acuminatus H. Adams, *Unio* : 1866, Proc. Zool. Soc. London, p. 376 ([Lake] Albert N'yanza [Central Africa]). Holotype BMNH 1867.1.9.4, figured by Smith, 1892, Ann. and Mag. Nat. Hist. (6) **10**, pl. 10, fig. 12, consists of one valve.

aegyptiaca Pallary, *Mutelina* : 1924, Mém. Inst. d'Egypt, **7** : 52, pl. 4, fig. 14 (Canal Mahmoudieh [Lower Nile, Egypt]). 2 Paratypes BMNH 1937.12.30. 13155-56.

aequatorius Morelet, *Unio* : 1885, Jour. de Conch., **33** : 31, pl. 2, fig. 9 (la rivière Mayumba, district de Cacongo [Congo] à 3 degrés au-dessus de l'Equateur). Holotype BMNH 93.2.4.1585 ; paratype BMNH 93.2.4.1586.

aereus Reeve, *Unio* : 1865, Conch. Iconica, **16**, *Unio*, pl. 30, species 160 (Hab.?, Cuming colln.). BMNH [lost].

- aeruginosus* Morelet, *Unio* : 1849, Testacea Novissima, **1** : 29 (rivulo Michol, circa Palenqueanum vicum [Chiapas, Mexico]). Measured holotype BMNH 93.2.4.2019, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 596, pl. 62, figs. 2, 2a, 2b ; paratype BMNH 93.2.4.2020.
- aethiopiiformis* "Ihering" Simpson, *Unio* : 1914, Descr. Cat. Naiades, **3** : 1312 [nomen nudum]. Specimens under this name, BMNH 1891.4.13.51–55. Distributed by Ihering but never described by him.
- aferula* Lea, *Unio* : 1864, Proc. Acad. Nat. Sci. Phila., **16** : 109 (Lake Nyassa, Central Africa, John Kirk) ; 1866 Jour. Acad. Nat. Sci. Phila. (2) **6** : 34, pl. 13, fig. 34 ; 1867, Obs. Unio, **11** : 38. Holotype USNM 84058 ; specimen from Kirk's lot, but not seen by Lea, BMNH 64.5.14.2.
- alata* Sowerby, *Hyria* : 1869, Conch. Iconica, **17**, *Hyria*, pl. 5, species 13 (Guayana). Holotype BMNH 1849.6.1.2 ; 2 paratypes BMNH 1849.6.1.2 1–2.
- alata* Lea, *Spatha* : 1864, Proc. Acad. Nat. Sci. Phila., **16** : 109 (Lake Nyassa, Central Africa, John Kirk) ; 1866, Jour. Acad. Nat. Sci. Phila. (2) **6** : 35, pl. 12, fig. 31 ; 1867, Obs. Unio, **11** : 39. Holotype USNM 86776 ; 2 specimens from Kirk's lot, but not seen by Lea, BMNH 62.9.25.4.
- ambiguus* "Parreyss" Philippi, *Unio* : 1847, Abb. und Besch. Conch., **3** : 7 [47], pl. 3, fig. 2. (Nova Hollandia, purchased from Parreyss). Holotype BMNH 41.4.29.103 *teste* and figured by McMichael and Hiscock, Australian Jour. Marine and F. W. Res., **9**, pl. 1, figs. 1–2. While there is no evidence that this specimen was the one figured by Philippi, it is probably as close to an authentic type as can be found.
- angasii* Sowerby, *Anodon* : 1870, Conch. Iconica, **17**, *Anodon*, pl. 32, species 127 (South Australia [Strangway's River, North Australia]). [Credited to Lea Obs., **12** but not described by him]. Holotype BMNH 70.10.26.41 refigured by McMichael and Hiscock, 1958, Australian Jour. Marine and F. W. Res., **9** : pl. 3, figs. 5–6.
- angustior* Hanley and Theobald, *Unio generosus* : 1872, Conch. Indica, p. 22, pl. 46, fig. 7 (Pegu) Holotype BMNH 1968655
- annulatus* Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 17, species 67 (Hab.?, Cuming colln.). BMNH [lost.]
- aplatus* Reeve, *Unio* : 1865, Conch. Iconica, **16**, *Unio*, pl. 28, species 143 (Island of Chiloe, Chili, Cuming colln.). BMNH [lost.]
- arcuans* Fischer and Crosse, *Unio calamitarum* : 1894, Miss. Sci. au Mexique, pt. 7, **2** : 613, pl. 64, figs. 5, 5a [Mexico, Morelet colln]. Figured holotype BMNH 93.2.4.2009.
- areolatus* Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 10, species 28 (Hab.?, Cuming colln.). BMNH [lost.]
- askewi* Marsh, *Unio* : 1896, Nautilus, **10** : 92 (Village Creek, Hardin Co., Texas ; Sabine River, Texas) ; Marsh 1897, Nautilus, **10** : 11, pl. 1, figs. 3–4. Figured holotype ANSP 70448a ; 2 paratypes BMNH 98.2.1.36–37, from the Sabine River, Texas.
- auklandicus* Gray, *Unio* : 1843 [in] Dieffenbach, Travels in New Zealand, **2** : 257 (Bay of Islands ; Auckland in the Bay of Amabrusa) restricted by McMichael and Hiscock 1958, Australian Jour. Marine and F. W. Res., **9** : 455 to near Auckland, North Island, New Zealand. Holotype BMNH 1951.9.6.17 figured *Ibid.*, pl. 12, figs. 13–14, is two unmatched valves original no. 1842.11.5.75.
- auratus* Reeve, *Unio* : 1865, Conch. Iconica, **16**, *Unio*, pl. 29, species 150 (Island of Chiloe, Chili, Cuming colln.). Holotype BMNH 1965144 ; 2 paratypes BMNH 1965145.
- auratus* Sowerby, *Unio* : 1866, Conch. Iconica, **16**, *Unio*, pl. 45, species 245 (South America, Hanley colln.). [not in BMNH].
- avae* Theobald, *Monocondylaea* : 1873, Jour. Asiatic Soc. Bengal, **42** (2) : 209, pl. 17, fig. 5 (Mandelay regno Birmanica). Figured holotype BMNH 88.12.4.1743.
- baikii* A. Adams, *Spatha* : 1866, Proc. Zool. Soc. London, p. 447 (River Niger [Nigeria]). Of the three syntypes of this species in the BMNH, one from the Cuming colln., is closest to Adams' original measurements and is, here selected, lectotype BMNH 196466, plate 1 fig. 3. Length 116, height 75, width 46 mm ; paralectotype BMNH 196467, Cuming colln. ; paralectotype BMNH 78.1.28.199. ex. A. Adams.

- bakeri**, H. Adams, *Unio* : 1866, Proc. Zool. Soc. London, p. 376 ([Lake] Albert N'yanza [Central Africa]). Holotype BMNH 1867.1.9.1, figured by Smith, 1892, Ann. and Mag. Nat. Hist. (6) **10**, pl. 12, fig. 11, consists of one valve.
- bambousearum** Morelet, *Anodon* : 1851, Testacea Novissima, **2** : 24 (rivulos prope vicum Palenqueanum, prov. Chiapas [Mexico]). Measured holotype BMNH 1965146, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 527, pl. 63, figs. 6, 6a.
- bellua** Morelet, *Anodonta* : 1866, Rev. et Mag. de Zool. (2) **18** : 167 (lacu Toui-Sap, [Cambodia]). Lectotype MCZ 175610 selected by Johnson, 1956, Bull. Mus. Comp. Zool. **115** : 107, pl. 1, fig. 1 ; paralectotype BMNH 1965147.
- bengalensis** Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 14, species 49 (Bengal Rivers, Cuming colln.). BMNH [lost].
- bhamoensis** Theobald, *Unio* : 1873, Jour. Asiatic Soc. Bengal, **42**(2) : 207, pl. 17, fig. 1 (prope Bhamo, Regno Birmanico ; necnon in Prome occidentali Provincia Pegu). Figured holotype BMNH 88.12.4.1672, refigured by Hanley and Theobald, 1876, Conch. Indica, p. 62, pl. 155, fig. 2 ; paratype BMNH 88.12.4.1673.
- bicaelatus** Reeve, *Unio* : 1865, Conch. Iconica, **16**, *Unio*, pl. 26, species 130 (Hab.?, Cuming colln.). BMNH [lost].
- bischoffi** "Ihering" Simpson, *Unio* : 1914, Descr. Cat. Naiades, **3** : 1312 [nomen nudum]. Specimens under this name, BMNH 1891.4.13.22-23, distributed by Ihering but never described by him.
- bonelli** Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 11, species 34 (Lago Maggiore [Italy] Cuming colln.). Holotype BMNH 1964379.
- breviculus** Call, *Unio* : 1887, Proc. United States Natl. Mus., **10** : 499, pl. 28 (Currant River, Shannon Co., Missouri and in Jack's Fork and Big Creek, tributaries of it). Holotype MCZ 5020 ; 2 paratypes BMNH 98.2.1.3940 from Big Creek.
- brevis** Sowerby, *Anodon* : 1870, Conch. Iconica, **17**, *Anodon*, pl. 31, species 124 (Rio Plata). Mentioned as in BMNH [lost].
- burtoni** Woodward, *Unio* : 1859, Proc. Zool. Soc. London, **27** : 349, pl. 47, fig. 1 (Lake Tanganyika [Central Africa]). Holotype BMNH 1859.12.23.9, refigured by Sowerby 1866, Conch. Iconica, **16**, *Unio*, pl. 47, species 251 ; paratype BMNH 1965220.
- calamitarum** Morelet, *Unio* : 1849, Testacea Novissima, **1** : 30 (rivulum Baluntie, prope Palenqueanum vicum [Chiapas, Mexico]). Not figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2**. Morelet gives the measurements of the type as : Altit. 29, latit. 51, diam. 16 mm. [not found]. Lectotype, here selected, BMNH 1893.2.4.2010, plate 2 fig. 5 Length 54, height 32, width 26 mm.
- callifera** Martens, *Anodonta* : 1860, Proc. Zool. Soc. London, **28** : 15 (Siam). Holotype BMNH 59.8.1.20, figured by Haas 1913, [in] Martini and Chemnitz, Conch. Cab. (2) **9**, pt. 2, sec. 2, pl. 46, fig. 3.
- cambojensis** Sowerby, *Unio* : 1866, Conch. Iconica, **16**, *Unio*, pl. 42, species 231 (Camboja, Cuming colln.). Holotype BMNH 1965148 consists of one valve ; 2 paratypes BMNH 1965149.
- carinthiacus** Ziegler, *Unio* : 1835 [in] Rossmässler, Icon. Land- und Susswasser Moll. (1) **1** : 21 ; *Ibid.*, **3** : 30, pl. 15, fig. 209 (Carinthia). Paratype BMNH 1965216, figured by Reeve, 1856, Conch. Iconica, **16**, *Unio*, pl. 30, species 157 [credited to Ziegler in index].
- carolinensis** Sowerby, *Castalia* : 1869, Conch. Iconica, **17**, *Castalia*, pl. 2, species 6 (South, Carolina). Holotype BMNH 1841.4.6.149.
- championi** Martens, *Unio* : 1900, Biol. Cent. Americana, Moll., p. 508, pl. 38, fig. 9, 9a (W. Guatemala : Paso Antonio, in the Pacific coast-region). Paratypes BMNH 1901.6.22.1538-9.
- charruana** Orbigny, *Unio* : 1835, Mag. de Zool., p. 35 (Banda orientali, republica Uruguayensi orientali) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 606, pl. 71, figs. 8-14 (tous les ruisseaux et les petites rivières depuis Maldonado, Montevideo, jusqu'à Las Bacas). Holotype BMNH 1854.9.4.15 from Rio Rosario ; 12 paratypes BMNH 1854.9.4.15/1-12.
- cheeziana** Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 15, species 52 (Hab. ?, Cuming Colln.). Holotype BMNH 1964399.

- chilensis** "Parreysis" Sowerby, *Unio* : 1867, Conch. Iconica, **16**, *Unio*, pl. 56, fig. 286 (Chili, Taylor colln.). Figured holotype BMNH 74.12.11.11.
- chinnerethensis** Preston, *Unio*. 1913, Jour. and Proc. Asiatic Soc. Bengal (n.s.) **9** : 473, pl. 27, fig. 10, 10a (Lake of Tiberias, Galilee). Paratypes BMNH 1913.7.30.18 ; 1914.1.7.203-205.
- chiquitana** Orbigny, *Anodonta* : 1835, Mag. de Zool., p. 41 (Corrientes, republica Argentina ; provincia Chiquitensi, rep. Boliviana). New name for *Anodon trigonum* Spix, pl. 22, fig. 2 ; 1846, Voy. Amér. Mérid., **5**, pt. 3, listed as a synonym of *Anodonta trigona* Spix.
- ciconia** Gould, *Anodon* : 1851, Proc. Boston Soc. Nat. Hist., **4** : 92 (Mexico?). Holotype MCZ 189084, figured by Johnson, 1964, Bull. United States Natl. Mus., 239, p. 54, pl. 34, fig. 1 ; paratype BMNH 1964397 figured by Sowerby, 1870, Conch. Iconica, **17**, *Anodon*, pl. 29, species 115a. Species 115b BMNH 1964389 is not this species.
- clappertoni** Koenig, *Anodon* : 1826 [in] Denham and Clapperton, "Narrative of Trav. and Discov. in N. and Centr. Africa, Appendix", p. 255 (Gammaroo River [appears to be a locality called Gamaroo on the Komadugu Yobe River, also called the Yaou or Yo]). Syntype BMNH [not catalogued].
- cochlearis** Sowerby, *Anodon* : 1870, Conch. Iconica, **17**, *Anodon*, pl. 33, species 135 (Hab. ?). BMNH [lost].
- cocoduensis** "White" Reeve, *Unio* : 1865, Conch. Iconica, **16**, *Unio*, pl. 24, species 117 (Hab. ?, Cuming colln.). Holotype BMNH 1965187 ; paratype BMNH 1965188.
- compressa** Martens, *Spatha* : 1860, Proc. Zool. Soc. London, **28** : 16 (Khaokho, NE of Pakpriau, Siam). Holotype BMNH 59.8.1.21, figured by Haas 1913, [in] Martini and Chemnitz, Conch. Cab. (2) **9**, pt. 2, sec. 2, pl. 36, fig. 2.
- contorta** Lea, *Triquetra* : see under, *lanceolata* Lea, *Triquetra*.
- cordata** Sowerby, *Castalia* : 1869, Conch. Iconica, **17**, *Castalia*, pl. 2, species 8 (British Guayana, Cuming colln.). Holotype BMNH 1965197 ; 2 smaller paratypes BMNH 1965198.
- coreanus** Martens, *Unio* : 1886, Sitzber. Gesell. Natur. Freunde, Berlin, p. 70 (Fluss Hangang, 15 km. oberhalb Söul [Prov. Kyongkwido] Korea) ; Martens, 1905, Zool. Jahrb., Suppl. 8, p. 50, pl. 3, fig. 5. Paratype BMNH 94.11.23.10.
- corium** Reeve, *Unio* : 1864, Conch. Iconica, **16**, *Unio* pl. 10, species 39 (Chiapa, Mexico, Cuming colln.). Holotype BMNH 1965209.
- corrientesensis** Orbigny, *Monocondylaea* : 1835, Mag. de Zool., p. 38 (Rio Corrientes, provincia Corrientesensi, republica Argentina) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 613, pl. 68, figs. 8-10 (le Rio Batel, au sud de la province de Corrientes, Argentine). Holotype BMNH 1854.9.4.28 ; 3 paratypes BMNH 1854.9.4.28/1-3.
- crepera** Lea, *Anodonta* : 1851 Proc. Zool. Soc. London for 1850, pt. 18, p. 198 (Bongabon, Luzon, Philippine Islands, Cuming) ; Lea, 1851, Ann. and Mag. Nat. Hist., **8** : 494 ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 238, pl. 23, fig. 117 ; Lea 1860, Obs. Unio, **7** : 56. Lea saw five or six specimens. Holotype BMNH [lost] ; 2 paratypes BMNH 1965158 ; paratypes USNM 86602. The two specimens in the BMNH 42.5.10.1538 labeled Saul, Luzon, are not types.
- crispata** Gould, *Unio* : 1843, Proc. Boston Soc. Nat. Hist., **1** : 141 ([Tavoy] British Burmah [Burma]). Lectotype MCZ 186099, selected by Johnson, 1964, Bull. United States Natl. Mus., 239, p. 62, pl. 32, fig. 3 ; paralectotype BMNH 1965223.
- crispisulcatus** Benson, *Unio* : 1862, Ann. and Mag. Nat. Hist., **10** : 193 ; Sowerby, 1866, Conch. Iconica, **16**, *Unio*, pl. 49, fig. 262 (Hab. ?, Cuming colln.). BMNH 1964358. Though credited to Lea ms., this specimen is probably a type.
- crocodilorum** Morelet, *Unio* : 1849, Testacea Novissima, **1** : 28 (flumen Usumasinta [Guatemala]). Measured holotype BMNH 93.2.4.2030, figured by Fischer and Crosse 1894, Miss. Sci. au Mexique, pt. 7, **2** : 577, pl. 60, fig. 3 ; 2 paratypes BMNH 93.2.4.2031-32, were also figured, pl. 60, figs. 4-5 and were named varieties *semipustulata* and *praestriata* respectively.
- cryptoradiata** Putzeys, *Spatha* : 1898, Ann. Soc. Mal. Belgique, **33** ; Bull. Séances, p. xxiv, figs. 14-15 (le Stanley-Pool, près de Leopoldville [Congo]). 2 paratypes BMNH 1902.11.20.1-2, from Putzeys, purchased from H. B. Preston.

- cumingii** Lea, *Anodonta* : 1850, Proc. Zool. Soc. London, **18** : 199 (Malacca, Cuming colln.) ; *cumingii* Lea, *Monocondylaea*, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 235, pl. 33, fig. 114 ; 1860, Obs. Unio, **7** : 53. Holotype USNM 86350 ; paratype BMNH [not catalogued] figured by Sowerby, 1870, Conch. Iconica, **17**, *Anodon*, pl. 31, species 122.
- cumingii** Dunker, *Galatea* ; 1860, [in] Bernardi, Monog. Galatea et Fischeria, p. 35, pl. 6, figs. 7-8 ; pl. 9, fig. 8 (le Gabon, Cuming colln.). BMNH [lost].
- cumingii** Lea, *Unio* : 1852, Proc. Acad. Nat. Sci. Phila., **6** : 54 (Northern part of China, H. Cuming) ; Lea 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 240, pl. 35, fig. 120 ; Lea 1860, Obs. Unio, **7** : 58. Holotype USNM 83897 ; paratype BMNH 1964360 figured by Sowerby, 1866, Conch. Iconica, **16**, *Unio*, pl. 49, species 264.
- cuneata** Preston, *Mutela* : 1910, Ann. and Mag. Nat. Hist. (8) **6** : 62, pl. 5, fig. 13 (Karonga, northern end of Lake Nyassa [Central Africa]). Paratype BMNH 1910.9.28.9.
- dactylus** Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 19, species 75 (Hab. ?, Cuming colln.). BMNH [lost].
- dactylus** Morelet, *Unio* : 1845, Moll. de Portugal, p. 110, pl. 14, fig. 2 (affluent de la Guadiana près de Castro-Verde en Algarve). Holotype BMNH 93.2.4.1587.
- dahomeyensis** Lea, *Anodonta* : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 154 (Dahomey, West Africa, Mr. Frazer, Cuming colln.) ; Lea 1859, Jour. Acad. Nat. Sci. Phila. (2) **4** : 261, pl. 41, fig. 141 ; Lea 1860, Obs. Unio, **7** : 79 ; Sowerby, 1870, Conch. Iconica, **17**, *Anodon*, pl. 36, species 151. Holotype BMNH 1965163. The type lot also contained two smaller specimens BMNH 1965164 not seen by Lea.
- dalyi** E. A. Smith, *Mulleria* : 1898, Proc. Mal. Soc. London, **3** : 14, text figs. (Probably near Mudgiri, Kadur District, Mysore Dist., Southern India). Lectotype BMNH 1897.11.19.1, selected by Pain and Woodward 1961, Jour. of Conch., **25** : 5, specimen in upper two drawings ; 2 paralectotypes BMNH 1897.11.30.19-20.
- delessertii** Bernardi, *Fischeria* : 1860, Monog. Galathea et Fischeria, p. 46, pl. 3, figs. 3-4 ; pl. 9, fig. 5 (Les cours d'eau près du cap Palmas, Guinée, Bernardi [Paris Mus.?] et Cuming colln.). BMNH [lost].
- delphinulus** Morelet, *Unio* : 1849, Testacea Novissima, **1** : 31 (paludosa flum. Usumasinta et lacum Petenensem [lac de Flores ou Tha, Guatemala]). The specimen figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 557, pl. 63, figs. 2, 2a, 2b in the Paris Museum may be a type, but it is larger than the measured holotype. Probable measured holotype BMNH 93.2.4.1588. Morelet's description gives Alt. 26, Lat. 60, Diam. 14 mm. The probable holotype measures, without the "wing", Length 29, height 60, width 14 mm. The label has the additional data given above in brackets.
- dembeae** Reeve, *Unio* : 1865, Conch. Iconica, **16**, *Unio*, pl. 29, species 153 (Dembea, Abyssinia, Cuming colln.). BMNH [lost].
- demeraraensis** Lea, *Unio* : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 152 (Demerara, British Guiana, Cuming colln.) ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 253, pl. 39, fig. 133 ; Lea, 1860, Obs. Unio, **7** : 71. Lea only saw the holotype, which was not found in the BMNH, or in the USNM.
- dernaica** Pallary, *Margaritana* : 1928, Jour. de Conch., **72** : 22, pl. 4, figs. 1-2 (l'oued Derna, affluent de la rive gauche de l'oum er Riba, à la hauteur de Tagnzirt (moyen Atlas, méridional) région de Tadla). Paratype BMNH 1937.12.30.13022.
- deviatus** "Anthony" Reeve, *Unio* : 1964, Conch. Iconica, **16**, *Unio*, pl. 15, species 61 (North America, Cuming colln.). Holotype BMNH 1965210, with Anthony's original label to H. Cuming, "Tennessee, very rare, best I have."
- digitatus** Morelet, *Unio* : 1851, Testacea Novissima, **2** : 24 (flumen Usumasinta [Peten Prov., Guatemala]). Measured holotype BMNH 93.2.4.2035, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 563, pl. 60, fig. 1.
- digitiformis** Sowerby, *Unio* : 1868, Conch. Iconica, **16**, *Unio*, pl. 65, species 333 (India, Taylor colln.). Holotype BMNH 1965199.
- diminutus** Lea, *Unio* : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 151 (East Africa, H. Cuming and S. Hanley) ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 254, pl. 39, fig. 134 ; Lea, 1860, Obs.

- Unio*, **7** : 72. Holotype BMNH 1965165 Cuming Colln. The type lot also contains a smaller specimen BMNH 1965166, not seen by Lea.
- dolabella* Sowerby, *Castalia* : 1869, Conch. Iconica, **17**, *Castalia*, pl. 3, species 13, figs. a-c (Hab.?, Cuming colln.). Holotype BMNH 1965185 [River Amazon]; paratype BMNH 1965186.
- dugasti* Morlet [sic], *Unio* : 1892, Jour. de Conch., **40** : 86 (rivière Outhene, petit affluent du Mékong, Laos); 1893, *Ibid.*, **41** : 156, pl. 6, fig. 4, 2 paratypes BMNH 93.12.8.137-8, ex. Ph. Dautzenberg.
- durrovensis* Phillips, *Margaritifera* : 1928, Proc. Mal. Soc. London, **18** : 72, pl. 3, fig. 1; pl. 4, fig. 1 (River Nore, Durrow, Queen's Co., England). 2 figured syntypes BMNH 1928.10.23. 1-2.
- dysonii* Lea, *Unio* : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 152 (Honduras, D. Dyson, Cuming colln.); Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 252, pl. 39, fig. 132; Lea, 1860, Obs. *Unio*, **7** : 70. Holotype BMNH 1965173. The type lot also contains a smaller specimen BMNH 1965174, not seen by Lea.
- electrinus* Reeve, *Unio* : 1865, Conch. Iconica, **16**, *Unio*, pl. 25, species 121 (Hab. ?, Cuming colln.). BMNH [lost].
- elliottii* Lea, *Unio* : 1856, Proc. Acad. Nat. Sci. Phila., **8** : 262 (Othcalooga Creek, Gordon Co., Georgia, Elliott); Lea, 1858, Jour. Acad. Nat. Sci. Phila. (2) **4** : 54, pl. 5, fig. 37; Lea, 1858, Obs. *Unio*, **6** : 54. Holotype USNM 84019; paratype BMNH 1965160, Cuming colln. ex Lea, figured by Reeve, 1864, Conch. Iconica, **16**, *Unio*, pl. 3, species 20.
- elongata* Longstaff, *Nodularia (Caelatura) parreysii* : 1914, Jour. Linn. Soc. London, **32** : 255, pl. 18, figs. 9-10 (White Nile River at Ad-Duwêm, Tawîla, and Gebel Ahmad Aghâ, Southern Sudân). Figured holotype BMNH 1923.6.8.1218 from Gebel Admad Aghâ.
- episcopalis* Tristram, *Unio* : 1865, Proc. Zool. Soc. London, p. 544 (Orontes River, Palestine). Lectotype, here selected, BMNH 1936.3.10.3. plate 2 fig. 1. Length 80, height 47, width 28 mm.
- esula* Orbigny, *Iridina* : 1835, Mag. de Zool. p. 43, *nomen nudum*; 1843, Voy. Amér. Mérid., **5**, pt. 3, p. 597 (tous les lacs du centre de la Bolivie; pays des Guarayos, province de Chiquitos, et dans toute la province de Moxos). The type was not figured, and since it was not found in the BMNH, it is presumed that it was lost between the time of description and the preparation of the plates.
- eurhynchus* "Bronn" Kuester, *Unio* : 1861 [in] Martini and Chemnitz, Conch. Cab. (2) **9**, pt. 2, p. 237, pl. 79, fig. 5 ([Minas Geraes] Brasilien). BMNH 1965217, distributed by Bronn before description by Kuester.
- evansi* Adams and Angus, *Unio* : 1864, Proc. Zool. Soc. London, p. 39 (Lagoons of Lower Murray R., South Australia). Holotype BMNH 1870.10.26.42, figured by McMichael and Hiscock, 1958, Australian Jour. Marine and F. W. Res., **9**, pl. 1, figs. 6-7.
- exasperata* Sowerby, *Hyria* : 1869, Conch. Iconica, **17**, *Hyria*, pl. 2, species 3 (British Guayana). BMNH [lost].
- exilis* Morelet, *Monocondylus* : 1866, Jour. de Conch., **14** : 63 (in torrentibus montanis Cambodiae [lac Toulis-sap au Combodje]). Holotype BMNH 93.2.4.1981, figured by Morelet, 1875, Séries Conch., pt. 4, p. 340, pl. 17, fig. 1.
- exoticus* Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 16, species 57 (Rio de la Plata [Argentina]). Holotype BMNH 1965207, consists of one valve.
- explicatus* Morelet, *Unio* : 1849, Testacea Novissima, **1** : 28 (flumen Usumasinta, ad pagum Balancan Tabascensium [Mexico]). Measured holotype BMNH 93.2.4.2027, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 594, pl. 61, fig. 1.
- expressa* Martens, *Anodonta* : 1900, Natur. Deutschen Mal. Ges., **32** : 12 (Lake Danau-Baru, Indragiri, Sumatra). Two syntypes are figured by Haas 1920, [in] Martini and Chemnitz, Conch. Cabinet **9**, pt. 2, no. 2, p. 304, pl. 38, figs. 1-2; syntype BMNH 1901.6.14.3.
- exulceratus* "Porro" Sowerby, *Anodon* : 1870, Conch. Iconica, *Anodon*, **17**, pl. 33, species 131. Figured holotype BMNH 1841.5.6.127, from Zeigler.
- faba* Orbigny, *Unio* : 1835, Mag. de Zool., p. 35 (Banda orientali, republica Uruguayensi

- orientali). Is a variety of *Unio charruana* Orb., *teste*, Orbigny, 1846, Voy. Amér. Mérid., 5, pt. 3, p. 606. 5 syntypes BMNH 1854.12.4.839.
- falcatus** Higgins, *Mycetopus* : 1868, Proc. Zool. Soc. London, p. 179, pl. 14, fig. 6 (Forest streams near Chyavetas, Upper Amazons [Brazil], E. Bartlett). Holotype BMNH 68.4.3.6 ; paratype MCZ 74218, ex. R. F. Geale.
- favidens** Benson, *Unio* : 1862, Ann. and Mag. Nat. Hist. (3) 10 : 188 (Ganges [River], between Cawnpore and Allahabad [India]). 2 syntypes BMNH 1965215 from Benson ex. Cuming colln. The type figured by Reeve, 1865, Conch. Iconica, 16, *Unio*, pl. 26, species 131 Cuming colln. BMNH [lost].
- ferrarisii** Orbigny, *Anodonta* : 1835, Mag. de Zool., p. 40 (Banda orientali [Rio del Rosario], Uruguayensi orientali) ; 1846, Voy. Amér. Mérid., 5, p. 615, pl. 74, fig. 3. Listed as synonym of *Anodontes sirionos* Orbigny. Figured holotype BMNH 1854.9.4.34, consists of one valve.
- fgdiana** Bloomer, *Caelatura aegyptiaca* : 1946, Proc. Mal. Soc. London, 27 : 69, pl. 6, fig. 3 (Wad Figda, canal between Khartoum and Sennaar, Soudan). Paratype BMNH 1948.5.58.
- fimbriata** Frierson, *Lampsilis* : 1907, Nautilus, 21 : 86, pl. 12, two upper figs. and lower left hand fig. (Valles River [San Luis Potosi Prov.] Mexico). Figured holotype Mus. Zool., Univ. Michigan 191161 ; 2 paratypes BMNH 1910.9.30.170-171.
- fluctiger**, Lea, *Unio* : 1859, Proc. Acad. Nat. Sci. Phila., 11 : 152 (Hab. ?, H. Cuming) ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) 4 : 250, pl. 39, fig. 130 ; Lea, 1860, Obs. Unio, 7 : 68. Refigured by Sowerby, 1866, Conch. Iconica, 16, *Unio*, pl. 42, species 299. Holotype BMNH 1965169. The type lot also contained a smaller specimen, BMNH 1965170 not seen by Lea.
- fontaineana** Orbigny, *Unio* : 1835, Mag. de Zool., p. 36 (Rio Parahiva, imperio Brasiliano) ; 1846, Voy. Amér. Mérid., 5, pt. 3, p. 605, pl. 69, figs. 6-7. Holotype BMNH 1854.9.4.49 ; paratype BMNH 1854.9.4.49/1.
- footei** Theobald, *Unio* : 1876, Jour. Asiatic Soc. Bengal, 45 (2) : 187, pl. 14, fig. 9 (Kistna flumine prope "Gutparba falls"). Figured holotype BMNH 88.12.4.1651.
- fossiculifera** Orbigny, *Monocondylaea* : 1835, Mag. de Zool., p. 38 (Rio Parana, provincia Corrientesensi, republica Argentina) ; 1846, Voy. Amér. Mérid., 5, pt. 3, p. 614, pl. 80, figs. 5-7 (Parana, à Iribucua, distant de vingt lieues au-dessus de corrientes, république Argentine). Holotype BMNH 1854.9.4.1 ; 7 smaller paratypes BMNH 1854.9.4.1/1-8.
- fragilis** Sowerby, *Unio* : 1865, Conch. Iconica, 16, *Unio*, pl. 30, species 155 (Island of Chiloe, Chili, Cuming colln.). Non *Unio fragilis* Swainson, 1823, changed to *Diplodon cuprinus* Simpson 1900, Proc. United States Natl. Mus., 22 : 883. Figured holotype BMNH [not catalogued] ; 2 paratypes [not catalogued].
- fragilis** Hanley and Theobald, *Unio corrugatus* : 1872, Conch. Indica, p. 21, pl. 45, fig. 4 (no locality). Figured holotype BMNH 196851.
- framesi** Connolly, *Indonaiia* : 1925, Records Albany [South Africa] Mus., 3 : 265, pl. 12, figs. 1, 4 (Transvaal : near Premier Mine, Pretoria Dist., South Africa). Holotype Senckenberg Mus.; paratypes BMNH 1926.7.7.8 and 1937.12.30.128.
- friersoni** Wright, *Unio* : 1896, Nautilus, 9 : 134, pl. 3 (Bayou Pierre, an arm of the Red River in DeSoto Parish, Louisiana). Lectotype USNM 133432, selected by Johnson, 1967, Occ. Papers on Moll., 3 : 6, pl. 5, fig. 4 ; 4 paralectotypes BMNH 98.2.1.43-44 and 05.8.15.38-39.
- fuligo** Reeve, *Unio* : 1865, Conch. Iconica, 16, *Unio*, pl. 30, species 159 (Hab. ?, Cuming colln.). BMNH [lost].
- fulmineus** "Parreyss" Philippi, *Unio* : 1847, Abb. und Besch. Conch., 3 : 6[46], pl. 3, figs. 5-6 (Nova Hollandia). 3 probable syntypes BMNH 41.4.18.135-138, from Parreyss.
- gibba** Sowerby, *Anodon* : 1867, Conch. Iconica, 17, *Anodon*, pl. 6, species 13 (River Kiang, [Vietnam] Cuming colln.). Holotype BMNH 1964372.
- gracilis** Lea, *Anodonta* : 1851, Proc. Zool. Soc. London for 1850, pt. 18, p. 197 (Dingle, Island of Panay, Philippine Islands, Cuming colln.) ; Lea, 1851, Ann. and Mag. Nat. Hist., 8 : 193 ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) 4 : 239, pl. 34, fig. 119 ; Lea, 1861, Obs. Unio, 7 : 57. Holotype USNM 86722 ; paratype BMNH [not found], figured by Sowerby, 1857, Conch. Iconica, 17, *Anodon*, pl. 14, species 45 ; 3 paratypes BMNH 1968657.

- gracilis* "Parreyss" Martens, *Iridina* : 1866, Mal. Blätt., **13** : 11 [nomen nudum, listed as a synonym of *Spathia rostrata* Rang] BMNH 41.4.28.152, distributed by Parreyss before description by Martens.
- graueri* Haas, *Caelatura* : 1927, Senckenbergiana, **9** : 21 (Urwald Ukaika, norwestlich vom Albert-Edward-See, Innerafrika). Paratype BMNH 1937.12.30.13117.
- grijalvae* Morelet, *Andonta* : 1884, Jour. de Conch., **32** : 123 (Rio dos Idolos, un des bras du fleuve Grijalva, Tabasco [Mexico]). Lectotype, here selected, BMNH 93.2.4.2009, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 532, pl. 59, fig. 1, consists of the opposite valve of the specimen figured by Fischer and Crosse and is somewhat smaller than the original measured type.
- guaraniana* Orbigny, *Unio* : 1835, Mag. de Zool., p. 37 (Rio Parana, provincia Corrientesensi, republica Argentina) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 608, pl. 69, figs. 10–12 (prés du village d'Itaty, Corrientes, lorsque le Parana, [Argentina]). Measured holotype BMNH 1854.12.4.841, the figure is enlarged ; paratype BMNH 1854.12.4.841/1, consists of one valve.
- guarayana* Orbigny, *Monocondylaea* : 1835, Mag. de Zool., p. 38 (Rio San Miguel, Guarayos [Chiquitos], Boliviana) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 614, pl. 68, figs. 4–7. Holotype BMNH 1854.9.4.17 ; paratypes BMNH 1854.9.4.17/1–3.
- guatybae* "Ihering" Simpson, *Unio* : 1914, Descr. Cat. Naiades, **3** : 1312 [nomen nudum]. Specimens under this name, BMNH 1891.14.13.34–37 were distributed by Ihering but never described.
- gubernaculum* Reeve, *Unio* : 1865, Conch. Iconica, **16**, *Unio*, pl. 28, species 146 (Hab. ?, Cuming colln.). Holotype BMNH 1965203 ; paratype BMNH 1965204.
- guppyi* E. A. Smith, *Unio* : 1885, Proc. Zool. Soc. London, p. 608, pl. 37, fig. 88a, b (Shortland Island, Solomon Islands). Figured holotype BMNH 1885.11.3.461 ; paratypes BMNH 1885.11.3.462–5.
- hanleyana* Sowerby, *Castalia* : 1869, Conch. Iconica, **17**, *Castalia*, pl. 1, species 5 (Hab. ?, Hanley colln.). Holotype BMNH 1900.3.19.5.
- hargerii* E. A. Smith, *Mutela* : 1908, Proc. Mal. Soc. London, **8** : 14, text fig. (Lake Mweru, Central Africa). Holotype BMNH 1907.11.11.55, consists of the one valve on which the description was based.
- harlandi* Baird and H. Adams, *Unio* : 1867, Proc. Zool. Soc. London, p. 492, pl. 26, fig. 3, 3a (Shanghai, North China). Figured holotype BMNH 1965222.
- herculeus* Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 3, species 7 ([Tago, Japan] Cuming colln.). Holotype BMNH 1965200, consists of one valve.
- hermosus* Bourguignat, *Unio* : 1889, Bull. Soc. Mal. de France, **6** : 38, new name for *Unio nyassaensis*, var. E. A. Smith 1881, Proc. Zool. Soc. London, p. 298, pl. 34, fig. 34b (Lake Nyassa). Holotype BMNH 1880.12.20.130, consists of one valve ; 2 paratypes BMNH 1880.12.20.131.
- hians* Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 4, species 8 (Hab. ?, Cuming Colln.). Holotype BMNH 1965205 ; paratype BMNH 1965206.
- horda* Gould, *Anodon* : 1855, Proc. Boston Soc. Nat. Hist., **5** : 299 (Comanche Creek, [Tributary of the Llando River, close to the present site of Mason, Mason Co.], Texas [teste Taylor, 1967, Veliger, **10** : 153]). Measured holotype USNM 678301 ; paratype BMNH 196465, figured by Sowerby, 1867, Conch. Iconica, **17**, *Anodon*, pl. 18, species 66, Cuming colln.
- horei* E. A. Smith, *Unio* : 1880, Ann. and Mag. Nat. Hist. (5) **6** : 429 (Lake Tanganyika [Central Africa]) ; 1881, Proc. Zool. Soc. London, p. 299, pl. 34, fig. 37. Holotype BMNH 80.12.20.42.
- humilior* Martens, *Unio scutum* : 1899, Archiv. für Natur., **1** : 45, pl. 5, fig. 1 (Chindwinfluss bei Kalewa und in einem Nebenfluss desselben, dem Yuffluss [Burma]). 4 paratypes BMNH 99.6.21.6–9.
- hyalaea* Orbigny, *Unio* : 1835, Mag. de Zool., p. 36 (provincia Chiquitensi, republica Boliviana) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 607, pl. 69, figs. 8–9 (Santa Cruz de la Sierra et de Chiquitos en Bolivia, principalement dans les rivières nommées Palometas, Pari, et Tucabaca). Holotype BMNH 1854.12.4.843, from Chiquitos ; paratype BMNH 1854.12.4.843/1, consists

- of one valve. Paratypes BMNH 1854.12.4.842 consists of two complete specimens and three odd valves from Santa-Cruz.
- impressa** Anthony, *Alasmodon* : 1865, Amer. Jour. Conch., **1** : 157, pl. 12, fig. 4 (Tennessee). Holotype MCZ 150666 ; 3 paratypes BMNH 1965152.
- indicus** Sowerby, *Unio* : 1866, Conch. Iconica, **16**, *Unio*, pl. 40, species 222 (India, Cuming colln.). Figured holotype BMNH 1965195 ; paratype BMNH 1965196.
- inflata** Orbigny, *Castalia* : 1835, Mag. de Zool., p. 43 (var. a, *rotunda*, provincia Corrientesensi, republica Argentina ; var. b, *elongata*, provincia Chiquitensi, republica Boliviana). Is *Castalia ambigua* Lamarck, *teste*, Orbigny, 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 598, pl. 72, figs. 4-7 ; 2 syntypes BMNH 1854.12.4.854, both figured.
- inornatus** Reeve, *Unio* : 1865, Conch. Iconica, **16**, *Unio*, pl. 29, species 147 (Cambodia, Cuming and Hanley collns.). Holotype BMNH [not catalogued] ; specimens from Hanley in ANSP 41673. Non *Unio inornatus* Lea 1856, changed to *Unio verus* by Lea, 1870, *Synopsis Unio*, p. 46.
- introrugatus** Connolly, *Unio* : 1931, Ann. and Mag. Nat. Hist., (10) **8** : 320, pl. 12, figs. 6-9 (Uganda : Victoria Nyanza). Holotype BMNH 1930.12.3.362 ; paratype BMNH 1930.12.3.363 and 1937.12.30.1327.
- involutus** "Benson" Hanley, *Unio* : 1856, Cat. Bivalve Shells, p. 385, pl. 23, fig. 17 (Assam, Hanley colln.). Figured holotype BMNH 1968656.
- iridella** Pilsbry and Frierson, *Lampsilis* : 1907, Nautilus, **21**, pl. 12, two lower right hand figs., 1908, *Ibid.* **22** : 81 (Valles, [San Louis Potosi Prov.] Mexico). Holotype ANSP 93810a ; paratype BMNH 1908.12.17.5.
- irisans** Marshall, *Anodontites* : 1926, Proc. United States Natl. Mus., **69** : 10, pl. 2, fig. 35 ; pl. 3, fig. 7 (Venezuela). Holotype USNM 359920 ; 2 paratypes BMNH 1926.2.3.29-30.
- japanensis** Lea, *Unio* : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 153 (Japan, Cuming colln.) ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 244, pl. 36, fig. 123 ; Lea, 1860, Obs. *Unio*, **7** : 62. Holotype BMNH 1965181.
- javana** Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 11, species 33 (Japan [error for Java *fide* original label] from Von dem Busch ; Cuming colln.). 3 syntypes BMNH 1965213, none agree exactly with the figure.
- johnstoni** E. A. Smith, *Unio (Metaptera)* ; 1893, Proc. Zool. Soc. London, p. 640, pl. 59, figs. 18-20 (Lake Mweru, British Central Africa). Figured holotype BMNH 93.8.23.100 ; paratype BMNH 93.8.23.101.
- jourdyi** Morlet [sic], *Anodonta* : 1886, Jour. de Conch., **34** : 76, pl. 15, fig. 1, 1a (Tonkin [North Vietnam] Environs de Lang-son, Chu). Syntype BMNH 1893.2.4.1395.
- kelletii** Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 19, species 71 (Hab. ?, Cuming colln.). Holotype BMNH 1964392.
- kirkii** Lea, *Unio* : 1864, Proc. Acad. Nat. Sci. Phila., **16** : 108 (Lake Nyassa, Central Africa, John Kirk) ; Lea, 1866, Jour. Acad. Nat. Sci. Phila. (2) **6** : 32, pl. 12, fig. 30 ; Lea, 1867, Obs. *Unio*, **11** : 36. Holotype USNM 84056 ; 2 separate valves BMNH 1965154, ex. Cuming colln. ; 2 specimens from Kirk's lot, but not seen by Lea, BMNH 62.9.25.7.
- laevis** Haas, *Ptychorhynchus* : 1910, Ann. and Mag. Nat. Hist. (8) **6** : 498 (Saghalim Island [Siberia]). Holotype Senckenberg Mus. 3626 ; 2 paratypes BMNH 1912.8.16.127-8 ; all ex Sowerby and Fulton.
- lampreyanus** Baird and Adams, *Unio* : 1867, Proc. Zool. Soc. London, p. 491, pl. 26, fig. 2 (Shanghai, North China). Figured holotype BMNH 67.5.13.16, also refigured by Sowerby 1868, Conch. Iconica, **16**, *Unio*, pl. 87, fig. 469, consists of one valve.
- lananensis** Frierson, *Quadrula* : 1901, Nautilus, **15** : 75, pl. 4. (Lanana and Banita Creeks near Nacogdoches [Nacogdoches Co.] Texas). Figured holotype ANSP 81561a ; 2 paratypes BMNH 1905.8.15.28-29.
- lanceolata** Lea, *Triquetra* : 1856, Proc. Acad. Nat. Sci. Phila., **8** : 79 (China?). Measured holotype USNM 83884. Changed by Lea to *Triquetra contorta*, 1856, Proc. Acad. Nat. Sci. Phila., **8** : 301 ; Lea, 1857, Jour. Acad. Nat. Sci. Phila. (2) **3** : 319, pl. 33, fig. 3 ; figured

- specimen BMNH 1964400 Shanghai [China], Cumming colln. Lea, 1857, Obs. Unio, **6**: 39. Refigured by Sowerby, 1869, Conch. Iconica, **17**, *Hyria*, pl. 1, species 2, figs. a–b.
- laosensis** Lea, *Unio*: 1863, Proc. Acad. Nat. Sci. Phila., **15**: 190 (Laos Mountains, Cambodia, Siam, from Mouhot in Cumming colln.); Lea, 1866, Jour. Acad. Nat. Sci. Phila. (2) **6**: 63, pl. 21, fig. 61; Lea, 1867, Obs. Unio, **11**: 67. Holotype USNM 86160. A supposed paratype figured by Sowerby, 1866, Conch. Iconica, **16**, *Unio*, pl. 47 species 256, BMNH 1964353, this lot also contains two other specimens which were not seen by Lea, who had but two specimens before him.
- latialata** Sowerby, *Hyria*: 1869, Conch. Iconica, **17**, *Hyria*, pl. 2, fig. 4 (British Guayana). Holotype BMNH 41.4.29.92; paratypes BMNH 41.3.6.30 and 41.3.6.33.
- layardii** Lea, *Unio*: 1859, Proc. Acad. Nat. Sci. Phila., **11**: 153 (Ceylon, from F. Layard, in Cumming colln.); Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4**: 243, pl. 36, fig. 122; Lea, 1861 Obs. Unio, **7**: 61. Holotype BMNH 1965159. This was the only specimen seen by Lea.
- legumen** Martens, *Anodonta*: 1888, Sitzber. Gesell. Natur. Freunde, Berlin, p. 65 (Banhados de S. Leopoldo, Prov. Rio Grande do Sul [Brazil]). Syntype BMNH 91.4.13.56.
- limnoica** Orbigny, *Anodonta*: 1835, Mag. de Zool., p. 40 (Lagunis, Provincia Corrientesensi, republica Argentina); 1846, Voy. Amér. Mérid., **5**, pt. 3, pl. 79, figs. 1–3. Holotype BMNH 1854.9.4.26; 4 paratypes BMNH 1854.9.4.26/1–4 all labeled, “Mayloya Corrientes.”
- linguaeformis** Morelet, *Anodonta*: 1875, Séries Conch., pt. 4, p. 329, pl. 14, fig. 5 (Cambodge, probablement dans les marécages voisins de Battambang). Holotype BMNH 93.2.4.612; 3 paratypes BMNH 93.5.12.19–21.
- luapulaensis** Preston, *Unio* (*Nodularia*): 1913, Rev. Zool. Africaine, **3**: 60, pl. 4, fig. 11 (Confluence of the Lukulu and Luapula Rivers, Belgian Congo). 2 paratypes BMNH 1913.7.30.24.
- lucasii** Morelet, *Anodon*: 1851, Jour. de Conch., **2**: 359 (les marécages boisés de La Calle [Algeria]). Measured holotype BMNH 93.2.4.1950 Pl. 1, fig. 2; paratype [not found] figured by Sowerby, 1867, Conch. Iconica, **17**, *Anodon*, pl. 17, species 64, sent to Cumming by Morelet. This appears to be a description of the shell figured, but not described, by Deshayes, 1848, Explor. Sci. de l’Algerie, Zool., **1**, pl. 108, figs. 1–2. If so, Deshayes’ named figure is a sufficient indication to afford him priority.
- lucida** Orbigny, *Anodonta*: 1836, Mag. de Zool., p. 40 (Banda orientali, republica Uruguayensi orientali); 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 620, pl. 79, figs. 4–6 (la rivière dite Canelon grande, Uruguay). Holotype BMNH 1854.12.4.834; 3 paratypes BMNH 1854.12.4.834/1–3 from the same lot labeled, “Rio del Rosario, Banda Orientali.”
- lukuluensis** Preston, *Mutela*: 1913, Rev. Zool. Africaine, **3**: 61, pl. 6, fig. 4 (Confluence of the Lukulu and Luapula Rivers, Belgian Congo). Paratype BMNH 1913.7.30.16.
- lurulentus** Morelet, *Anodon*: 1849, Testacea Novissima, **1**: 28 (in paludibus fluvii Usumasinta [Peten Prov., Guatemala]). Measured holotype BMNH 93.2.4.2003, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2**: 523, pl. 64, fig. 6; 2 paratypes BMNH 93.2.4.2004–5. The original label reads, “Marais de San Geronimo” [Yucatan, Mexico].
- macilenta** Morelet, *Anodonta*: 1845, Moll. de Portugal, p. 102, pl. 11 (à une lieue de Coimbre, dans de profonds marécages voisins du Mondégo et connus sous le nom de Val de Géria [Portugal]). Syntype BMNH 93.2.4.1678.
- mainwairingi** “Nevill” Preston, *Unio*: 1912, Records Indian Mus., Calcutta, **7**: 306 (Siliguri; also Namtsik, Diha[o]ng [River]). Holotype Indian Mus., figured by Preston 1915, Fauna of British India, Pelecypoda, p. 191, fig. 24; 5 paratypes BMNH 91.3.6.3–7.
- mandarinus** Morelet, *Unio*: 1864, Jour. de Conch., **12**: 159 (Cochinchina [South Vietnam]); 3 syntypes BMNH 93.2.4.1971–3; Morelet, 1875, Séries Conch., pt. 4, p. 354, pl. 17, fig. 2. Listed as a synonym of *U. scobinatus* Lea.
- mandalayensis** Theobald, *Unio*: 1874, Jour. Asiatic Soc. Bengal, **42** (2): 208, pl. 17, fig. 2 (prope Mandalay, regno Birmanico). Figured holotype BMNH 1888.12.4.2018; paratype BMNH 1888.12.4.2019, figured by Hanley and Theobald, 1876, Conch. Indica, p. 62, pl. 154, fig. 4.

- marocana** Pallary, **Margaritana** : 1918, Bull. Soc. Hist. Nat. Afrique du Nord. **9** : 152 (l'oued Fès [Maroc]). 2 syntypes BMNH 1937.12.30.13034-13035.
- marteli** Pallary, **Unio** : 1918, Bull. Soc. Hist. Nat. Afrique du Nord, **9** : 151 (La Makina à Fès [Maroc]). 2 syntypes BMNH 1937.12.30.13036-13037.
- martensi** Ihering, **Castalina** : 1893, Archiv für Natur., **59** (1) 81, pl. 3, fig. 5 (Rio Camaquã, Rio Grande do Sul, Brazil). Lectotype Senckenberg Mus. 3785, selected by Haas, 1931, Senckenbergiana **13**: 41; 2 paralectotypes BMNH 91. 4. 13. 57-58.
- mashonae** Preston, **Unio** : 1910, Ann. and Mag. Nat. Hist. (8) **6** : 61, pl. 4, fig. 10 (a sluit about 16 miles from Eukeldoorn, Mashonaland [South Rhodesia]). Holotype BMNH 1910.1.15.6; paratypes BMNH 1910.1.15.7-12.
- massini** Morelet, **Unio** : 1864, Jour de Conch., **12** : 288 (Cochinchina [South Vietnam]). Holotype BMNH 93.2.4.1590, figured by Morelet, 1875, Séries Conch., pt. 4, p. 348, pl. 15, figs. 1, 3; 2 paratypes BMNH 93.2.4.1591-2.
- matoniana** Orbigny, **Unio** : 1835, Mag. de Zool., p. 35 (Rio de la Plata, republica Argentina). Is **Unio variabilis** Wood, teste Orbigny, 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 604, pl. 71, figs. 1-3. Holotype BMNH 1854.9.4.50; paratypes BMNH 1854.9.4.50/1-9.
- mauritanus** Lea, **Unio** : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 152 (Island of Mauritius, Cuming colln.); Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 257, pl. 40, fig. 138; Lea, 1860, Obs. **Unio**, **7** : 75. Holotype BMNH 1965157.
- melleus** Lea, **Unio** : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 152 (*Hab.*? [Mexico or Central America], Cuming colln.); Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 250, pl. 38, fig. 129; Lea, 1860, Obs. **Unio**, **7** : 68; Reeve, 1865, Conch. Iconica, **16**, **Unio**, pl. 21, species 92. Holotype BMNH 1965175; also a smaller specimen BMNH 1965176, not seen by Lea.
- menzieianus** "Gray" Reeve, **Unio** : 1865, Conch. Iconica, **16**, **Unio**, pl. 29, species 152 (New Zealand, Cuming colln.). BMNH [lost] [is **Unio menziesi** Gray].
- menziesi** Gray, **Unio** : 1843, [in] Dieffenbach, Travels in New Zealand **2** : 257 (Lake Taupo, North Island, New Zealand, restricted by Dell, 1953, Trans. Royal Soc. New Zealand, **81** : 229). Holotype BMNH 42.5.17.170, figured by McMichael and Hiscock, 1958, Australian Jour. Marine and F. W. Res., **9**, pl. 14, figs. 1-2.
- merdiger** Reeve, **Unio** : Conch. Iconica, **16**, **Unio**, pl. 28, species 145 (Hungary, Cuming colln.). Holotype BMNH 1964161.
- mexicanus** Sowerby, **Unio** : 1867, Conch. Iconica, **16**, **Unio**, pl. 55, species 281 (Mexico, Taylor colln.). Holotype BMNH 79.2.26.249.
- micans** Anthony, **Anodon** : 1865, Amer. Jour. Conch., **1** : 162, pl. 16, fig. 1 (Texas). Holotype MCZ 187290; paratype BMNH 1968652 figured by Sowerby 1867, Conch. Iconica, **17**, **Anodon**, pl. 15, species 53.
- micropterus** Morelet, **Unio** : 1866, Jour. de Conch., **14** : 63 (in torrentibus montanis Cambodiae). Measured holotype BMNH 93.2.4.1596, figured by Morelet, 1875, Séries Conch., pt. 4, p. 349, pl. 15, fig. 6 (the figure is reduced); paratype BMNH 93.2.4.1597.
- minuana** Orbigny, **Monocondylaea** : 1835, Mag. de Zool., p. 37 (Uruguayensis orientali republica); 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 612, pl. 70, figs. 8-10 (dans les rivières de Canelon Grande et del Rosario, dans la Banda oriental do la Plata, Uruguay). Holotype BMNH 1854.9.4.17; 2 paratypes BMNH 1854.9.4.27/1-2.
- misellus** Morelet, **Unio** : 1865, Jour. de Conch. **13** : 21 ([Salaburi] Siam). Holotype BMNH 93.2.4.1593, figured by Morelet, 1875, Séries Conch., pt. 4, p. 341, pl. 14, fig. 2; 2 paratypes BMNH 93.2.4.1994-5.
- moretonicus** Sowerby, **Unio** : 1865, Conch. Iconica, **16**, **Unio**, pl. 24, species 118 (Moreton Bay, Australia). Holotype BMNH 1958.5.16.1.
- morini** Morelet, **Unio** : 1851, Testacea Novissima, **2** : 25 (flumen Usumasinta [Peten Prov., Guatemala]). Measured holotype BMNH 93.2.4.2026, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 576, pl. 60, fig. 2, pl. 67, fig. 4.
- mouhoti** Lea, **Monocondylaea** : 1863, Proc. Acad. Nat. Sci. Phila., **15** : 190 (Laos Mountains, Cambodia, Siam); changed without explanation to:
- mouhotiana** Lea, **Monocondylaea** : 1866, Jour. Acad. Nat. Sci. Phila. (2) **6** : 65, pl. 21, fig.

- 62; Lea, 1867, Obs. Unio, **11**: 69. Holotype USNM 86339; paratype BMNH [not catalogued].
- mucidus** Morelet, *Unio*: 1845, Moll. de Portugal, p. 111, pl. 14, fig. 3 (La Taméga, le Cavado et la Lima [Rivers, Portugal]). Holotype BMNH 93.2.4.1974; paratype BMNH 93.2.4.1975, both from le Cavado. The holotype is the measured specimen. The figure appears to be a composite of both specimens; 2 additional paratypes BMNH 93.2.4.1979-80 from Rio Taméga and Mondago.
- mutabilis** Lea, *Unio*: 1859, Proc. Acad. Nat. Sci. Phila., **11**: 152 (Brisbane water, Australia; New Zealand, H. Cuming; Murray River, Australia, W. Newcomb); Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4**: 248, pl. 38, fig. 127; Lea, 1860, Obs. Unio, **7**: 60. Figured holotype BMNH [lost] from New Zealand. Lectotype, here selected, BMNH 1965153 from Brisbane water, figured by Reeve, 1865, Conch. Iconica, **16**, *Unio*, pl. 24, species 112. It was refigured by McMichael and Hiscock, 1958, Australian Jour. Mar. F. W. Res., **9**: 449, pl. 11, fig. 11; paralectotype USNM 85815, *Ibid.*, pl. 11, figs. 8-9; paralectotype USNM 84405, from Murray River.
- mweruensis** E. A. Smith, *Unio*: 1908, Proc. Mal. Soc. London, **8**: 13, text figs. (Lake Mweru, Central Africa). Figured syntype BMNH 1907.11.11.34; also syntypes BMNH 1907.11.33.35-49.
- navigioliformis** Lea, *Unio*: 1859, Proc. Acad. Nat. Sci. Phila., **11**: 152 (Hab. ?, Cuming colln.); Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4**: 248, pl. 37, fig. 124; Lea, 1860, Obs. Unio, **7**: 63. Holotype, and only specimen seen by Lea, not found in the BMNH or in the USNM.
- nehringi** Ihering, *Castalina*: 1893, Archiv. für Natur., **59**(1): 75, pl. 3, fig. 4 (Rio Piracicabo, São Paulo, Brazil). Lectotype Senckenberg Mus. 3787, selected by Haas, 1931, Senckenbergiana **13**: 41; paralectotype BMNH 1891.4.13.116.
- nehringi** Ihering, *Glabaris*: 1893, Archiv für Natur., **59**(1): 60 (Rio St. Maria, Rio Grande do Sul; [Rio] Piracicaba, São Paulo, Brazil). 3 paratypes BMNH 1891.4.13.107-109.
- nopalatensis** Sowerby, *Anodon*: 1867, Conch. Iconica, **17**, *Anodon*, pl. 16, species 58 (River Nopalata, Mexico). Holotype BMNH 1965189, consists of opposite of figured valve only.
- novaeahollandiae** Gray, *Unio*: 1834, Proc. Zool. Soc. London, pt. 2, p. 57 (in novae Hollandiae flumine Macquarrier [probably Port Macquarie, Hastings River, N. coast of New South Wales]). Syntypes BMNH 1880.4.10.6-7, consisting of 2 left valves, figured by McMichael and Hiscock 1958, Australian Jour. Mar. and F. W. Res., **9**: 474, pl. 15, figs. 1-2.
- nyassae** Sowerby, *Unio*: 1866, Conch. Iconica, **16**, *Unio*, pl. 41, species 224, figs. a, b (Lake Nyassa, [Central Africa] Cuming colln.). BMNH [lost].
- nyassaensis** Lea, *Spatha*: 1864, Proc. Acad. Nat. Sci. Phila., **16**: 109 (Lake Nyassa, Central Africa, John Kirk); Lea, 1866, Jour. Acad. Nat. Sci. Phila. (2) **6**: 36, pl. 13, fig. 33; Lea, 1867, Obs. Unio, **11**: 40. Holotype USNM 86777; specimen from Kirk's lot, but not seen by Lea, BMNH 1864.5.14.1.
- nyassaensis** Lea, *Unio*: 1864, Proc. Acad. Nat. Sci. Phila., **16**: 108 (Lake Nyassa, Central Africa, John Kirk); Lea, 1866, Jour. Acad. Nat. Sci. Phila. (2) **6**: 33, pl. 12, fig. 32; Lea, 1867, Obs. Unio, **11**: 40. Holotype USNM 84057; specimen from Kirk's lot but not seen by Lea, BMNH 1864.5.14.3.
- obesa** Hanley and Theobald, *Unio marginalis*: 1872, Conch. Indica, p. 20, pl. 43, fig. 3 (River Irawadi, Birmah). Figured holotype BNMH 1907.12.30.46; idio type BMNH 88.12.4.1642, from Tonyhu, Pegu ex Theobald.
- obicularis** Morelet, *Monocondylus*: 1866, Rev. et Mag. de Zool. (2) **18**: 167 (no locality [Battambang, Cambodge]). Measured holotype BMNH 93.2.4.1982, figured by Morelet, 1875, Séries Conch., pt. 4, p. 338, pl. 16, fig. 5, the figure is slightly enlarged.
- obliqua** Longstaff, *Nodularia* (*Caelatura*) *parreysii*: 1914, Jour. Linn. Soc. London, **32**: 255, pl. 18, fig. 11 (White Nile River at Tawili, Masran Island and Melût, Southern Sudan). Figured holotype BMNH 1923.6.8.1214, from Melût.
- obliquiradiatus** Reeve, *Unio*: 1865, Conch. Iconica, **16**, *Unio*, pl. 29, species 151 (Hab. ?, Cuming colln.). BMNH [lost].

- obliterata* Fischer and Crosse, *Unio scutulatus* : see under *scutulatus* Morelet, *Unio*.
- oleivorus* Heude, *Mycetopus* : 1877, Conch. Fluv. Nanking, pt. 3, pl. 22, fig. 46 ; pl. 23, fig. 48 (La Hoai supérieure, département de Ing-tch'eu [China]). BMNH 99.4.22.69, labeled Ngan-houé, from R. P. Heude in 1878, ex A. Morelet colln. Not a primary type.
- ortmanni* Frierson, *Unio* : 1913, Nautilus, **27** : 14, pl. 2 (Conchins River, near Quirigua, Guatemala [Atlantic Drainage]). Figured holotype ANSP 177544a ; 3 paratypes BMNH 1914.1.7.305-307.
- ostreatus* Morelet, *Unio* : 1849, Testacea Novissima, **1** : 29 (flumen Usumasinta [Peten Prov., Guatemala]). Measured holotype BMNH 94.3.22.2, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 573, pl. 63, fig. 3, pl. 70, fig. 4.
- ovata* Sowerby, *Castalia* : 1869, Conch. Iconica, **17**, pl. 1, species 4 (Brazil, Orbigny colln.). Holotype BMNH 1964402.
- ozarkensis* Call, *Unio* : 1887, Proc. United States Natl. Mus., **10** : 498, pl. 27 (Currant River, Shannon Co., Missouri, and in Jack's Fork and Big Creek, tributaries of it). Holotype MCZ 5707 ; paratype BMNH 98.2.1.41, localities not separated.
- pahangensis* E. A. Smith, *Unio* : 1899, Proc. Mal. Soc. London, **3** : 315, text fig. (Pahang River, Malay Peninsula). Figured holotype BMNH 99.9.4.1.
- paivaeanus* Morelet, *Unio* : 1865, Jour. de Conch., **13** : 227 (Siam [rivière Saraburi]). Holotype BMNH 93.2.4.1738, figured by Morelet, 1875, Séries Conch., pt. 4, p. 353, pl. 17, fig. 7, where it is listed as a synonym of *U. rusticus* Lea.
- pajakomboensis* Bullen, *Unio* : 1906, Proc. Mal. Soc. London, **7** : 15, pl. 2, figs. 9-11 (River at Pajakombo, Sumatra). Figured holotype BMNH 1906.1.16.52.
- pallaryi* Longstaff, *Nodularia (Lanceolaria) teretiuscula* : 1914, Jour. Linn. Soc., London, **32** : 256, pl. 18, figs. 12-14 (White Nile River, Mogran, Southern Sudan). Figured holotype BMNH 1923.6.8.1214.
- pallegoixi* Sowerby, *Anodon* : 1865, Conch. Iconica, **17**, *Anodon*, pl. 8, species 18, fig. 17 (Siam, Cuming colln.). Holotype BMNH 1965193 ; paratype BMNH 1965194.
- pallida* Anthony, *Anodon* : 1865, Amer. Jour. Conch., **1** : 162, pl. 15, fig. 3 (Michigan). Holotype MCZ 161871 ; 3 paratypes BMNH 1965155.
- paludosus* Morelet, *Unio* : 1849, Testacea Novissima, **1** : 30 (paludosa prope San Geronimo Yucataneorum [Mexico]). Measured holotype BMNH 93.2.4.2024, figured by Fischer and Crosse 1894, Miss. Sci. au Mexique, pt. 7, **2** : 559, pl. 59, fig. 3.
- panacoensis* Von dem Busch, *Unio* : 1843 [in] Philippi, Abb. und Besch. Conch., **1** : 75, pl. 2 (flumen Panaco prope Tampico [Mexico]). Paratype BMNH 1965183.
- papyracea* Anthony, *Anodon* : 1865, Amer. Jour. Conch., **1** : 161, pl. 15, fig. 2 (Hab. ? [Potomac River, Virginia]). Holotype MCZ 150656 ; 3 paratypes BMNH 1965151.
- paraguayana* Orbigny, *Monocondylaea* : 1835, Mag. de Zool., p. 37 (Rio Parana [près du village d'Itaty] et Rio Batel, provincia Corrientesensi, republica Argentina) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 612, pl. 70, figs. 5-7. Holotype BMNH 1854.9.4.13 ; 4 paratypes 1854.9.4.13/1-4.
- parchappii* Orbigny, *Monocondylaea* : 1835, Mag. de Zool., p. 38 (Rio Parana, provincia Corrientesensi, republica Argentina) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 613, pl. 68, figs. 1-3 (sous les pierres de la côte du Parana, aux environs d'Itaty, province de Corrientes, Argentine). Holotype BMNH 54.9.4.29 ; 7 paratypes BMNH 1854.9.4.29/1-7.
- parma* "Benson" Sowerby, *Unio* : 1868, Conch. Iconica, **16**, *Unio*, pl. 95, species 514 (Tennaserim, East Indies, Hanley colln.). Figured holotype BMNH 88.12.4.1669 ; refigured by Hanley and Theobald 1876, Conch. Indica, p. 61, pl. 154, fig. 1.
- patagonica* Orbigny, *Unio* : 1835, Mag. de Zool., p. 37 (Rio Negro, Patagonia) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 610, pl. 70, figs. 1-4. Figured holotype BMNH 1854.12.4.850 ; 7 paratypes BMNH 1854.12.4.850/1-7 ; 5 smaller paratypes BMNH 1854.12.4.851.
- pellis-lacerti* Morelet, *Unio* : 1865, Jour. de Conch., **13** : 27 (Siam [dans le rivière de Saraburi ; Cambodge, dans celle de Battambang, et en Cochinchine, près de Mitho]). Holotype BMNH 93.2.4.1969, figured by Morelet, 1875, Séries Conch., pt. 4, p. 356, pl. 17, fig. 5, paratypes BMNH 93.2.4.1966-8 and 1970, all from the first locality.

- persulcatus** Lea, *Unio* : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 153 (Mexico, Hanley colln.) ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 255, pl. 40, fig. 135 ; Lea, 1860 Obs. *Unio*, **7** : 73. Holotype BMNH 1900.3.19.22.
- pinei** Wright, *Unio* : 1897, Nautilus, **11** : 40 (unnamed lake in Witthacoochee [Withlacoochee] River region of Hernando Co., Florida). Holotype USNM 150127, figured by Simpson 1900, Proc. Acad. Nat. Sci. Phila., **52** : 80, pl. 3, fig. 1 ; refigured by Johnson 1967, Occ. Papers on Moll., **3** : 8, pl. 10, fig. 5 ; 2 paratypes BMNH 1905.8.15.34-35.
- piracicabana** Ihering, *Unio aethiops* : 1893, Archiv. für Natur., **59** (2) : 102 ([Rio] Piracicaba, São Paulo, Brazil). Holotype Senkenberg Mus. 4031 ; 2 paratypes BMNH 91.4.13.119-120.
- planivalvis** Morelet, *Unio* : 1851, Testacea Novissima, **2** : 24 (in paludibus fluminis Usumasinta vicinis [Peten Prov., Guatemala]). Measured holotype BMNH 93.2.4.2025, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 560, pl. 59, fig. 2. The original label reads, "Marais de S. Geronimo" [Yucatan, Mexico].
- plexoides** Frierson, *Psoronaias* : 1927, Check List North American Naiades, p. 63. Based on Sowerby, 1868, Conch. Iconica, **16**, *Unio*, pl. 64, species 324 (Siam, Taylor colln.). Not known if ever in BMNH.
- plicatulus** Lea, *Unio* : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 152 (Borneo, Cuming colln.) ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 247, pl. 37, fig. 126 ; Lea, 1860, Obs. *Unio*, **7** : 65. Holotype BMNH 1965156.
- plicatus** Leach, *Dipas* : 1814, Zool. Miscellany, **1** : 120, pl. 55 (Hab. ?, British Museum). Holotype BMNH 1952.5.10.1 from the Hans Sloane colln., consisting of two unmatched valves, refigured by Wilkins, 1953, Bull. Brit. Mus. Nat. Hist., Hist. Ser., **1** : 40, pl. 12.
- plicatus** Sowerby, *Mycetopus* : 1868, Conch. Iconica, **16**, *Mycetopus*, pl. 2, species 3 (Hab. ?). Holotype BMNH 46.7.24.18 ; paratype BMNH 46.7.24.19.
- pliciferus** Reeve, *Unio* : 1864, Conch. Iconica, **16**, *Unio*, pl. 10, species 37 (Mexico, Cuming colln.). BMNH [lost].
- pliculosus** Martens *Unio* : 1894, Sitzber. Gesell. Natur. Freunde, Berlin, p. 216 (Singei [Prov. Hwanghaido] (a) und zwischen Okkwa und Chhangpyöng (b) ersteres im südlichen letzteres im nördlichen Theil von Korea) ; Martens, 1905, Zool. Jahrb., Suppl. 8, p. 61, pl. 3, figs. 3, 3b. Paratype BMNH 94.11.24.8, from locality (b).
- praestricta** Fischer and Crosse, *Unio crocodilorum* : see under *crocodilorum* Morelet, *Unio*.
- pressorstris** Martens, *Unio* : 1900, Natur. Deutschen Mal. Ges., **32** : 14 (Lake Danau-Baru, Indragiri, Sumatra). Measured holotype figured by Haas 1914, [in] Martini and Chemnitz, Conch. Cabinet (2) **9**, pt. 2, sec. 2, p. 227, pl. 27, fig. 1 ; paratype BMNH 1901.6.14.4.
- prolongata** Fischer and Crosse, *Unio calamitarum* : 1894, Miss. Sci. au Mexique, pt. 7, **2** : 613, pl. 63, figs. 5, 5a ([Mexico] Morelet colln.). Figured holotype BMNH 93.2.4.2009.
- psammoica** Orbigny, *Unio* : 1835, Mag. de Zool., p. 35 (Rio Parana, provincia Corrientesensi, republica Argentina) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 608, pl. 71, figs. 4-7 (la Parana, près du village d'Itaty, bien au-dessus de Corrientes). Lectotype, here selected BMNH 54.12.4.849, which is the specimen figured on pl. 71, figs. 4-6 ; 2 smaller paralectotypes BMNH 1854.4.12.849/1-2, the smallest specimen is figured on pl. 71, fig. 7.
- psoricus** Morelet, *Unio* : 1851, Testacea Novissima, **2** : 25 (flumen Usumasinta [Peten Prov., Guatemala]). Measured holotype BMNH 93.2.4.2033, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 572, pl. 61, fig. 3 ; paratype BMNH 93.2.4.2034.
- puelchana** Orbigny, *Anodonta* : 1835, Mag. de Zool., p. 40 (Rio Negro, Patagonia) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 620, pl. 79, figs. 7-9 (les marais de San-Xavier, à six lieues au-dessus du Carmen, sur le Rio Negro, Patagonie). Holotype BMNH 1854.9.4.21 ; 3 smaller paratypes [under same number].
- punctatus** Preston, *Mycetopus* : 1909, Ann. and Mag. Nat. Hist. (8) **3** : 513, pl. 10, fig. 8 (Rio Chemchi, U.S. Columbia). Figured holotype BMNH 1915.1.6.83.
- quadrata** Sowerby, *Castalia* : 1869, Conch. Iconica, **17**, *Castalia*, pl. 2, species 7, figs. a-b (Hab. ?). Figured holotype BMNH 49.1.5.5.
- quadrilatera** Orbigny, *Castalia* : 1835, Mag. de Zool., p. 42 (provincia Moxensi, republica Boliviana) ; 1846, Voy. Amér. Mérid. **5**, pt. 3, p. 599, pl. 73 (Rio de San-Miguel, Guarayos,

- Bolivia). Lectotype, here selected, BMNH 54.9.4.2 the largest specimen figured; figured paralectotype BMNH 1854.9.4.2/1; 6 paralectotypes BMNH 1854.9.4.2/2-7.
- ranarum** Morelet, *Anodonta*: 1845, Moll. de Portugal, p. 104, pl. 12, fig. 2 (affluens de la Guadiana qui descendent des hautes-vallées de l'Algarve entre Mertola et Castro-Verde [Portugal]). Holotype BMNH 93.2.4.1737.
- ravistellus** Morelet, *Unio*: 1849, Testacea Novissima, 1: 29 (in lacu Yzabal, republicae Guatemalensis). Measured holotype BMNH 93.2.4.2021, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, 2: 509, pl. 61, fig. 4; 2 paratypes BMNH 93.2.4.2022-3.
- recta** Sowerby, *Hyria*: 1869, Conch. Iconica, 17, *Hyria*, pl. 5, species 10 (Hab. ?, Cuming colln.). BMNH [lost].
- rectilinearis** Sowerby, *Unio*: 1868, Conch. Iconica, 16, *Unio*, pl. 65, species 332 (River Columbia [South Africa] Taylor colln.). Holotype BMNH 74.12.11.4.
- regularis** Morelet, *Anodonta*: 1845, Moll. de Portugal, p. 100, pl. 10 (La Taméga . . . aux environs de Chavès [Portugal]). Syntype BMNH 93.2.4.1679.
- reticulatus** Sowerby, *Anodon*: 1867, Conch. Iconica, 17, *Anodon*, pl. 10, species 27 (River Amazon [Brazil], Cuming colln.). Holotype BMNH 1965208.
- rhuacoica** Orbigny, *Unio*: 1835, Mag. de Zool., p. 36 (Banda orientali, republica Uruguayensi orientali); 1846, Voy. Amér. Mérid., 5, pt. 3, p. 606, pl. 69, figs. 4-5; pl. 71, figs. 12-14 (un ruisseau près de Maldonado, et dans le Rio Canelon grande près de Montevideo, Uruguay). Lectotype, here selected, BMNH 1854.12.4.838 specimen figured on pl. 69, figs. 4-5; paralectotypes BMNH 1854.12.4.838/1-3 all from the latter locality.
- riograndensis** Ihering, *Anodonta*: 1890, Archiv. für Natur., 56 (1): 154 ([Rio Camaquã] Rio Grande do Sul; und dem Plata Gebeite, Brazil). Holotype Senkenberg Mus, 3838; 4 paratypes BMNH 91.4.13.15-18, localities not separated.
- robsoni** Frierson, *Parreysia*: 1927, Check List of North American Naiades, p. 44. (East Indies). Name based on shell figured by Reeve, 1866, Conch. Iconica, 16, *Unio*, pl. 36, species 198 as *Unio pumilis* Lea. Holotype BMNH 1965150.
- rosea** Bernardi, *Galatea concamerata*: 1860, Monog. Galatea et Fischeria, p. 20, pl. 3, figs. 1-2 ([Africa] Cuming colln.). BMNH [lost].
- rostratus** Sowerby, *Anodon*: 1867, Conch. Iconica, 17, *Anodon*, pl. 2, species 4 (Lao, Sowerby colln.). 3 syntypes BMNH 1965214 all smaller than figured specimen.
- rotundatus** Reeve, *Unio*: 1865, Conch. Iconica, 16, *Unio*, pl. 23, species 106 (North America, Cuming colln.). BMNH [lost].
- rugatus** Sowerby, *Mycetopus*: 1868, Conch. Iconica, 16, *Mycetopus*, pl. 3, species 7 (Victoria River, Australia). Lectotype BMNH 44.1.12.160, selected by McMichael and Hiscock, 1958, Aust. Jour. Marine and F. W. Res., 9: 433, pl. 9, figs. 1-2.
- sacculus** "Anthony" Reeve, *Unio*: 1864, Conch. Iconica, 16, *Unio*, pl. 15, species 67 (North America, Cuming colln.). BMNH [lost].
- santa-mariae** Simpson, *Diplodon*: 1914, Descr. Cat. Naiades, 3: 1270 (Brazil?). Specimens BMNH 1891.4.13.24-26, from Rio St. Maria, Rio Grande do Sul, Brazil, distributed by Ihering but never described by him.
- scamnatus** Morelet, *Unio*: 1849, Testacea Novissima, 1: 30 ([Rio Las Pazas] Cacajajicara, [Pinar del Rio] Cuba). Lectotype, here selected, BMNH 1893.2.4.1976, labeled, "Rio Tacotaco," [Pinar del Rio] Cuba, plate 2 fig. 3. Length 52, height 34, width 17 mm; paralectotypes BMNH 1893.2.4.1977-78, one of which consists of one valve.
- schadei** Marshall, *Anodontites*: 1943, Jour. Washington Acad. Sci., 24: 78 [unnumbered plate], figs. 4-6 (Tubicuary River, Aroja, Paraguay). Holotype USNM 434732; paratype USNM 434837, the only specimens seen by Marshall, who received them from Fulton; 2 additional specimens BMNH 1934.7.3.20-21.
- schombergiana** Sowerby, *Castalia*: 1869, Conch. Iconica, 17, *Castalia*, pl. 1, species 3 (British Guayana, Schomberg). Holotype BMNH 1841.1.26.5.
- schomburgianus** Sowerby, *Anodon*: 1870, Conch. Iconica, 17, *Anodon*, pl. 34, species 137 (British Guiana, Schomberg). BMNH [lost].
- schomburgki** Martens, *Anodonta (Lamproscapha)*: 1860, Proc. Zool. Soc. London, 28: 15

- (Siam). Holotype BMNH 59.5.23.8, figured by Haas, 1920, [in] Martini and Chemnitz, Conch. Cab. (2) **9**, pt. 2, sec. 2, p. 296, pl. 36, fig. 4.
- scriptus** Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 4, species 9 (Hab. ?, Cuming colln.). Holotype BMNH 1964370.
- scutulatus** Morelet, *Unio* : 1849, Testacea Novissima, **1** : 30 (propre S. Geronimo, Yucatan-eorum [Mexico]). Measured holotype BMNH 93.2.4.2014, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 561, pl. 59, fig. 4 ; 2 paratypes BMNH 93.2.4.2017-18 BMNH 1893.2.4.2015-16 were also figured, pl. 59, figs. 5 and 6, and named varieties *obliterata* and *secabilis* respectively.
- scutum** Sowerby, *Unio* : 1868, Conch. Iconica, **16**, *Unio*, pl. 94, species 510 (Tenasserium, Hanley colln.). Holotype BMNH 1907.10.28.239.
- secabilis** Fischer and Crosse, *Unio scutulatus* : see under *scutulatus* Morelet, *Unio*.
- semicorrugata** Preston, *Spatha* : 1909, Ann. and Mag. Nat. Hist. (8) **4** : 90, pl. 4, fig. 7 (Lower Congo). Paratype BMNH [not catalogued].
- semigranosus** Reeve, *Unio* : 1864, Conch. Iconica, **16**, *Unio*, pl. 10, species 36 (Mexico, Cuming colln.). Holotype BMNH 196496. *Non Unio semigranosus* Von dem Busch 1845.
- semipustulata** Fischer and Crosse, *Unio crocodilorum* : See under *crocodilorum* Morelet, *Unio*.
- semiquadrata** Sowerby, *Unio* : 1866, Conch. Iconica, **16**, *Unio*, pl. 48, species 258 (Camboja, Lao Mountains, Cuming colln.). BMNH [lost].
- semisulcata** H. Adams, *Monocondylaea (Plagiodon)* : 1870, Proc. Zool. Soc. London, p. 376, pl. 27, fig. 3 (East Peru). Syntype BMNH 1907.10.28.128, smaller than figured specimen.
- senegalensis** Lea, *Anodonta* : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 154 (Senegal, Jay, Verreaux, Cuming) ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 260, pl. 41, fig. 140 ; Lea, 1860, Obs. *Unio*, **7** : 78. Sowerby, 1867, Conch. Iconica, **17**, *Anodon*, pl. 11, species 35. Holotype BMNH 1965167 ; paratype BMNH 1965168.
- senilis** Martens, *Spatha trapezia* : 1897, Bes. Weicht. Deutsch-Ost-Afrikas, p. 244, text fig. (Victoria Nyansa, Nordwestseite, bei Towalio, Buddu Küste, und Insel Soweh in Uganda). Paratype BMNH 1902. 5.26.45. from Buddu Küste.
- servatiana** Bourguignat, *Grandidieria* : 1885, Bull. Soc. Mal. de France, **2** : 6. Name based on shell figured as *Unio burtoni* Smith 1881, Proc. Zool. Soc. London, p. 297, pl. 34, fig. 33, *non* Woodward 1859. Figured holotype BMNH 80.12.20.21.
- shambiensis** Longstaff, *Nodularia (Caelatura)* : 1914, Jour. Linn. Soc. London, **32** : 253, pl. 18, figs. 4-7 (Lake Shâmbê [Bahrel-Gebel] Southern Sudân). 3 paratypes BMNH 1923.6.8. 1214-16.
- shanghaiensis** Lea, *Unio* : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 153 (Shanghai, China, Cuming) ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 242, pl. 36, fig. 121 ; Lea, 1860, Obs. *Unio*, **7** : 60. Reeve, 1865, Conch. Iconica, **16**, *Unio*, pl. 21, fig. 96. Holotype BMNH 1965171 ; a smaller specimen not seen by Lea BMNH 1965172.
- siculus** Swainson, *Unio* : 1840, Treatise on Malacology, p. 282, fig. 58. Hanley, 1856, Cat. Recent Bivalve Shells, p. 383, Supp. pl. 20, fig. 19 (Lake Leontini, Sicily). Probable syntype BMNH 1907.10.28.255, *fade* Hanley. Probable syntype figured by Sowerby, 1868, Conch. Iconica, **16**, *Unio*, pl. 71, species 255, BMNH 1907.12.30.366 ex Hanley colln.
- sikkimensis** Lea, *Unio* : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 151 (Sikkim, India, Cuming and Hanley) ; Lea, 1859, Jour. Acad. Nat. Sci. Phila. (2) **4** : 251, pl. 39, fig. 131 ; Lea, 1860, Obs. *Unio*, **7** : 69. Holotype BMNH 1965177 Cuming colln. ; a second specimen not seen by Lea BMNH 1965178 ; paratype BMNH 1900.3.19.23 Hanley colln.
- siliquosus** Orbigny, *Mycetopoda* : 1835, Mag. de Zool., p. 41 (provincia Corrientesensi, republica Argentina ; Santa-Cruz de la Sierra, republica Boliviana) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 601, pl. 67 (le cours de Parana, province de Corrientes, république Argentine ; tous les affluens de l'Amazone, provinces de Santa-Cruz de Chiquitos et de Moxos, république de Bolivia) [not located]. *Non* Spix 1827, teste Ihering 1910, Abh. Senckenb. Ges., **32**, p. 121 and named *Mycetopoda orbigny*. Paratype BMNH [not located] figured by Sowerby 1868, Conch. Iconica, **16**, *Mycetopus*, pl. 3, species 2, fig. 2a.

- simonis* Tristram, *Unio* : 1865, Proc. Zool. Soc. London, p. 544 (the Jordan, the sea of Galilee, the Orontes and the Leontes [Litany] [Palestine]). Measured holotype BMNH 1936.3.10.6, plate 2 fig. 2 from the Orontes River.
- simplicidus* Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 12, species 40 (Hab. ?, Taylor colln.). Not known if ever in BMNH.
- singleyanus* Marsh, *Unio* : 1891, Nautilus, **5** : 29, figured by Simpson, Proc. United States Natl. Mus., **15** : 426, pl. 68, figs. 4, 5 (a small creek near Pilatka [Palatka, Putnam Co.] Florida). Idiotype BMNH 98.2.1.42, from Sumter Co., Florida.
- sirionos* Orbigny, *Anodonta* : 1835, Mag. de Zool., p. 40 (var. Major, provincia Chiquitensi, Boliviana ; var. Minor, provincia Corrientesensi, republica Argentina) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 615, pl. 74, figs. 4-6 ; pl. 80, figs. 1-4 (le Rio Canelon Grande, près de Montevideo, du Parana, au-dessus de Corrientes, près du village d'Itaty, Argentina et dans le Rio de San-Miguel, au pays des Guarayos, province de Chiquitos, et dans le Piray, province de Santa-Cruz en Bolivia). Holotype BMNH 54.9.4.9 ; 6 smaller paratypes BMNH 1854.9.4.9/1-6 all from le Rio-San-Miguel au pays des Guarayos, Chiquitos ; 3 paratypes BMNH 1854.9.4.35-36.
- sitifensis* Morelet, *Unio* : 1851, Jour. de Conch., **2** : 360 (l'oued sefsaf, près de Philippeville ; [Algeria]). Lectotype, here selected, BMNH 93.2.4.1965, plate 2 fig. 6, labeled Algerie, "l'oued dehhah, près de Bone [sic]". Length 71, height 33, width 23 mm.
- smithi* Bourguignat, *Grandidieria* : 1885, Bull. Soc. Mal. de France, **2** : 7. Name based on shell figured as *Unio burtoni* Smith 1881, Proc. Zool. Soc. London, p. 297, pl. 34, fig. 33a, non Woodward 1859. Figured holotype BMNH 80.12.20.31.
- sobaensis* Preston, *Nodularia* : 1914, Jour. Linn. Soc. London, **32** : 266, pl. 18, figs. 1-3 (Soba, Blue Nile). Figured holotype BMNH 1923.6.8.1210 ; 2 paratypes BMNH 1923.6.8.1211-1212.
- solenidea* Sowerby, *Anodon* : 1867, Conch. Iconica, **17**, *Anodon*, pl. 18, species 65 (Rio Francisco [Brazil] Cuming colln.). Holotype BMNH 1965201 ; paratype BMNH 1965202.
- soleniformis* Orbigny, *Anodonta* : 1835, Mag. de Zool., p. 41 (no locality) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 617, pl. 74, figs. 1-3 (Iribucua, dans le Parana, bien audessus de Corrientes ; et dans le Rio Balel [Argentina]). Holotype BMNH 1854.12.4.857 and paratypes BMNH 1854.12.4.857/1-10, from the first locality.
- soleniformis* Orbigny, *Mycetopus* : 1835, Mag. de Zool., p. 41 (Santa-Cruz de la Sierra, rep. Boliviana) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 601, pl. 66 (Rio Piray, entre Santa-Cruz de la Sierra et la province de Moxos, Bolivia). Holotype BMNH 1854.12.4.859, the figure is slightly reduced ; paratypes BMNH 1854.12.4.859.
- solisiana* Orbigny, *Unio* : 1835, Mag. de Zool., p. 36 (Rio de la Plata, in provincia Buenos-Ayres republica Argentina) ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 604, pl. 69, figs. 1-3 (plages sablonneuses de la Plata, aux environs de Buenos-Ayres ; elle y est très-commune, surtout à l'embouchure des petites ruiaux, de ceux de Punta Lara et de Maldonado [Argentina]). Holotype BMNH 1854.9.4.47 ; 11 paratypes BMNH 1854.9.4.48, localities not separated.
- spekii*, Woodward, *Iridina* (*Pleiodon*) : 1859, Proc. Zool. Soc. London, **27** : 348, pl. 27, fig. 2 (Lake Tanganyika [Central Africa]). Holotype BMNH 1859.12.23.8, refigured by Sowerby 1866, Conch. Iconica, **16**, *Pleiodon*, pl. 1, species 2.
- spheniopsis* Morelet, *Unio* : 1849, Testacea Novissima, **1** : 29 (regiones superiores fluminis Usumasinta [Penten Prov., Guatemala]). Measured holotype BMNH 93.2.4.2028, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, **2** : 583, pl. 61, figs. 2, 2a, 2b ; smaller paratype BMNH 93.2.4.2029.
- spixii* Orbigny, *Anodonta* : 1835, Mag. de Zool., p. 39 (Rio-Parana, provincia Corrientesensi, republica Argentina). New name for *Anodon rotundum* Spix ; 1846, Voy. Amér. Mérid., **5**, pt. 3, p. 619, listed as a synonym of *Anodonta trapezum* Spix. BMNH [lost].
- staudingeri* Ihering, *Mycetopus* : 1890 Archiv. für Natur., **56** (1) : 131, figs. a-b (Oberen Amazonas, und seiner Zuflüsse von Ecuador und Peru). Lectotype Senckenberg Mus. 3802, selected by Haas, 1931, Senckenbergiana **13** : 103 ; 3 paratypes BMNH 1902.11.20.3-4 ; 1902.9.2.35

- stuarti** A. Adams and Angus, *Unio* : 1864, Proc. Zool. Soc. London, p. 417 (lagoon, near Mt. Margaret, Central Australia). Holotype BMNH 1870.10.26.40, figured by McMichael and Hiscock, Australian Jour. Marine and F. W. Res., 9, pl. 2, figs. 10-11.
- subcrassa** Lea, *Anodonta* : 1850, Proc. Zool. Soc. London, p. 198 ; 1851, Ann. and Mag. Nat. Hist., 8 : 495 ; 1859, Jour. Acad. Nat. Sci. Phila. (2) 4 : 236, pl. 33, fig. 115 ; 1860, Obs. Unio, 7 : 54 (Laguna de Bai, Luzon, Philippine Islands, Cuming colln.). Holotype USNM 86693 ; 2 paratypes BMNH 42.5.10.1529 Cuming colln., one figured by Sowerby, 1877, Conch. Iconica, 17, *Anodon*, pl. 42, species 42.
- subjecta** Iredale, *Centralhyria angasi* : 1934, Australian Zool., 8 : 67, based in part on shell figured by Smith, 1874, Zool. of "Erebus" and "Terror" : Mollusca, p. 3, pl. 4, fig. 2. Selected as lectotype BMNH 40.10.21.29, by McMichael and Hiscock, 1958, Australian Jour. Marine and F. W. Res., 9 : 427, pl. 8, figs. 6-7 (Avon River, Western Australia).
- subreniformis** Sowerby, *Anodon* : 1867, Conch. Iconica, 17, *Anodon*, pl. 14, species 50 (Lake Nyassa, Cuming colln.). Holotype BMNH 1965192.
- subsinuatus** Sowerby, *Anodon* : 1867, Conch. Iconica, 17, *Anodon*, pl. 7, species 14 (Hab. ?, Cuming colln.). BMNH [lost].
- subtortus** Baird and Adams, *Unio* : 1867, Proc. Zool. Soc. London, p. 491, pl. 26, figs. 1, 1a (Shanghai, North China). Holotype BMNH 1867.5.18.17, refigured by Sowerby 1868, Conch. Iconica, 16, *Unio*, pl. 87, species 465.
- subtrigonus** Sowerby, *Unio* : 1867, Conch. Iconica, 16, *Unio*, pl. 58, species 292 (Siam, Taylor colln.). Holotype BMNH 1874.12.11.3.
- swainsoni** Sowerby, *Unio* : 1868, Conch. Iconica, 16, *Unio*, pl. 76, fig. 396 (Hab. ?, Hanley colln.). Holotype BMNH 1900.3.19.21.
- swinhoei**, H. Adams, *Anodonta* : 1866, Proc. Zool. Soc. London, p. 446 (Formosa). Probable measured holotype BMNH 78.1.28.200 ; smaller paratype BMNH 78.1.28.201.
- swinhoei** Sowerby, *Unio* : 1866, Conch. Iconica, 16, *Unio*, pl. 42, species 232 (Camboja, Capt. Swinhoe, Cuming colln.). Holotype BMNH 1968653.
- syriaca** Pallary, *Margaritana* : 1929, Mém. Inst. d'Egypte, 12, 34, text-fig. (Nahr el-Kébir, 30 km. au Sud de Tartous [Syria]). 2 paratypes BMNH 1937.12.30.13052-3.
- tabascensis** Morelet, *Anodonta* : 1884, Jour. de Conch., 32 : 124 (Marais du Tabasco [Mexico]). Holotype BMNH 93.2.4.2008, figured by Fischer and Crosse, 1894, Miss. Sci. au Mexique, pt. 7, 2 : 530, pl. 62, fig. 1.
- tabula** Sowerby, *Anodon* : 1867, Conch. Iconica, 17, *Anodon*, pl. 18, species 68 (Sierra Leone, Cuming colln.). Holotype BMNH 1965190 ; paratype BMNH 1965191.
- tanganyicensis** E. A. Smith, *Spatha* : 1880, Proc. Zool. Soc. London, p. 350, pl. 31, figs. 8, 8a. (Lake Tanganyika [Central Africa]). Lectotype, here selected, BMNH 80.3.5.48, specimen in figure 8 ; paralectotypes BMNH 80.3.5.49-53.
- tanganyicensis** E. A. Smith, *Unio* : 1880, Proc. Zool. Soc. London, p. 351, pl. 32, figs. 9, 9a (Lake Tanganyika [Central Africa]). Lectotype, here selected, BMNH 80.3.5.39 specimen in figure 9 ; paralectotypes BMNH 80.3.5.40-47.
- tanganyicensis** E. A. Smith, *Unio nyassaensis* : 1881, Proc. Zool. Soc. London, p. 298, pl. 34, fig. 34a (Lake Tanganyika [Central Africa]). Figured holotype BMNH 1880.12.20.39, consists of one valve : paratypes BMNH 1880.12.20.40-41, consists of two valves ; 3 paratypes BMNH 1880.12.10.130-131, consists of 3 odd valves.
- tauriformis** Fulton, *Unio (Cumeopsis)* : 1906, Ann. and Mag. Nat. Hist. (7) 17 : 246, pl. 9, fig. 9 (Yunnah-fu, Yunnan [China]). Holotype BMNH 1906.5.8.72.
- tavoyensis** Gould, *Unio* : 1843, Proc. Boston Soc. Nat. Hist., 1 : 140 ([Tavoy] British Burmah [Burma]). Measured holotype MCZ 169389 figured by Johnson, 1964, Bull. United States Natl. Mus., 239, p. 156, pl. 32, fig. 4 ; paratypes BMNH 1965184, largest one figured by Reeve, 1864, Conch. Iconica, 16, *Unio*, pl. 13, species 49.
- tenuis** Lea, *Anodonta* : 1851, Proc. Zool. Soc. London for 1850, pt. 18, p. 198 (Sual, Luzon, Philippine Islands, Cuming) ; Lea 1851, Ann. Mag. Nat. Hist. (2) 8 : 494 ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) 4 : 232, pl. 33, fig. 116 ; Lea, 1860, Obs. Unio, 7 : 55. Lea had 4 specimens before him. The holotype was not found in the BMNH. Paratype BMNH

- 1968654; paratype USNM 86764; 4 specimens under this name, MCZ 175578, ex Cuming. A specimen was figured by Sowerby, 1867, *Conch. Iconica* 17, *Anodon*, pl. 15, species 55, from the Cuming colln. but it was not the holotype.
- testudineus** Morelet, *Unio*: 1841, *Testacea Novissima*, 1: 28 (flumen Usumasinta [Peten Prov., Guatemala]). Measured holotype BMNH 94.3.22.1, figured by Fischer and Crosse, 1894, *Miss. Sci. au Mexique*, pt. 7, 2: 571, pl. 62, fig. 3. The specimen figured by Reeve, 1865, *Conch. Iconica*, 16, *Unio*, pl. 22, species 101, from the Cuming colln. has Morelet's label, but it is not this species.
- thomsoni** E. A. Smith, *Unio*: 1880 *Ann. and Mag. Nat. Hist.* (5) 6: 430 (Lake Tanganyika [Central Africa]); Smith, 1881, *Proc. Zool. Soc. London*, p. 299, pl. 34, fig. 36. Holotype BMNH 80.12.20.36; 2 paratypes BMNH 80.12.20.37-38.
- thwait[e]sii** Lea, *Unio*: 1859, *Proc. Acad. Nat. Sci. Phila.*, 11: 152 (Ceylon, Mr. Thwaites, H. Cuming); Lea, 1860, *Jour. Acad. Nat. Sci. Phila.* (2) 4: 246, pl. 37, fig. 125; Lea, 1860, *Obs. Unio*, 7: 64; Reeve, 1865, *Conch. Iconica*, 16, *Unio*, pl. 23, species 105. Holotype BMNH 1965179. Two smaller specimens not seen by Lea, BMNH 1965180.
- tortuosus** Sowerby, *Unio*: 1868, *Conch. Iconica* 16, *Unio*, pl. 65, species 330 (Maryland, Taylor colln.). Holotype BMNH 74.12.11.25.
- trapezia** Martens, *Spatha*: 1897, *Bes. Weich. Deutsch-Ost-Afrikas*, p. 243, text fig. (Victoria-Nyansa im Süden bie Bussisi; im Südwesten bei Nyemirembe und Nyamagotso; im Westen bie Bare an der Buddu-Küste; bei Bukoba; Mhugu an der Ostseite des Sees). Paratype BMNH 1902.5.26.44 from the second locality.
- trapezialis** Orbigny, *Iridina*: 1835, *Mag. de Zool.*, p. 43; 1846, *Voyage Amér. Mérid.*, 5, pt. 3, p. 596, (les bords du Parana, au-dessus de la ville de Corrientes, et aux environs de la Bajada, province d'Entre-Rios, république Argentine), non *Anodonta trapezialis* Lamarck *teste* Orbigny. Not figured by Orbigny and not found in the BMNH.
- triangularis** Sowerby, *Anodon*: 1867, *Conch. Iconica*, 17, *Anodon*, pl. 15, species 56: (Hab. ?, Cuming colln.). 1870 *Ibid.*, pl. 29, fig. 56b. The second specimen figured, was selected as "Lectotype" BMNH 1968211, by Sowerby, and is the only specimen extant.
- triostriis** Benson, *Unio*: 1863 [in] Hanley, *Photographic Conch.*, pl. 2, fig. 9 (no locality [Hindostan]). Figured holotype BMNH 1907.2.30.45.
- tristis** Morelet, *Unio*: 1845, *Moll. de Portugal*, p. 107, pl. 13, fig. 2 (à peu distance d'Amarante, au bord de la Taméga [Portugal]). Holotype BMNH 93.2.4.1961.
- tsadianus** Martens, *Unio (Grandidieria)* 1903, *Sitzber. Gesell. Natur. Freunde, Berlin*, p. 8 (südufer des Tsad-Sees [Borneo]). Paratype BMNH 1904.4.29.17.
- tumens** Haas, *Anodontites lautus*: 1910, *Ann. and Mag. Nat. Hist.* (8) 6: 499 (Yamashira, Japan). Holotype Senckenberg Mus. 3671, ex. Sowerby and Fulton; 2 paratypes BMNH 1912.8.16.123-4.
- tumidus** Morelet, *Monocondylus*: 1866, *Jour. de Conch.*, 14: 62 (in torrentibus montanis Cambodiae). Holotype BMNH 93.2.4.1734, figured by Morelet, 1875, *Séries Conch.*, pt. 4, p. 337, pl. 16, fig. 1; 2 paratypes BMNH 93.2.4.1735; 93.2.4.1566.
- tunizana** Morelet, *Anodonta*: 1864, *Jour. de Conch.*, 12: 156 (La Calle [Tuniza]). Lectotype, here selected, BMNH 1893.2.4.1964, plate 2 fig. 4. Length 55, height 32, width 20 mm.
- turcicus** "Parreiss" [sic] Kuester, *Unio*: 1862 [in] Martini and Chemnitz, *Conch. Cab.* (2) 9, pt. 2, p. 267, pl. 90, figs. 3-4 (Kleinasien). 2 specimens BMNH 47.5.28.1-2, distributed by Parreyss before description by Kuester.
- unicolor** Bernardi, *Galatea kochii*: 1860, *Monog. Galatea et Fischeria*, p. 23, pl. 4, figs. 3-4. ([Central Africa] Cuming colln.). BMNH [lost].
- vaalensis** Chaper, *Unio*: 1885, *Bull. Soc. Zool. France*, 10: 480, pl. 11, figs. 1-3 (Le Vaal (Afrique australe) auprès de Barclay à peu distance des mines de diamant du Griqualand West) Paratype BMNH 1937.12.30.1314.
- vellicatus** Reeve, *Unio*: 1865, *Conch. Iconica*, 16, *Unio*, pl. 22, species 103 (Guatemala, Cuming colln.). BMNH [lost].
- ventricosus** Orbigny, *Mycetopus*: 1846, *Voy. Amér. Mérid.*, 5, pt. 3, p. 602, pl. 72, figs. 1-3

- (province de Chiquitos, république de Bolivie, aux sources de Rio de Tucabaca, non loin de la mission de San-Juan). BMNH [lost].
- verecundus** Gould *Unio* : 1850 Proc. Boston Soc. Nat. Hist., **3** : 295 (Manila [Philippine Islands]) ; Gould 1852, United States. Expl. Exped., **12** : 431, pl. 37, figs. 541, a-c. Figured holotype USNM 5926 ; paratype BMNH 1964150, figured by Reeve 1865, Conch. Iconica, **16**, *Unio*, pl. 25, species 125.
- verrucifer** Martens, *Unio* : 1894, Sitzber. Gesell. Natur. Freunde, Berlin, p. 216 (Fluss Hangang [bei Soul, Prov. Kyongkwido], Korea) ; Martens, 1905, Zool. Jahrb., Suppl. 8, p. 61, pl. 3, figs. 2, 2b. Paratype BMNH 94.11.24.9, consists of one valve.
- vignouana** Bernardi, *Margaritana* : 1858, Jour. de Conch., **7** : 302, pl. 10, fig. 1 (un lac vosin de la rivière Como, Haut Gabon). Figured holotype and two paratypes in colln. of Jour de Conch., Paris teste Fischer, 1950, Jour. de Conch., **90** : 18 ; paratype BMNH [lost] figured by Reeve, 1865, Conch. Iconica, **16**, *Unio*, pl. 25, species 120 as *Unio vignonana*.
- vittatus** Lea, *Unio* : 1859, Proc. Acad. Nat. Sci. Phila., **11** : 153 (Australia, H. Cuming) ; Lea, 1860, Jour. Acad. Nat. Sci. Phila. (2) **4** : 249, pl. 38, fig. 128 : Lea, 1860, Obs. Unio, **7** : 67. Opposite valve of type also figured by Reeve, 1864, Conch. Iconica, **16**, *Unio*, pl. 18, species 83, Holotype BMNH 1958.4.3.1 ; paratype USNM 84407. See discussion by McMichael and Hiscock, 1958, Australian Jour. of Marine and F. W. Res., **9** : 390, pl. 2, fig. 1, pl. 1, figs. 13-14.
- vonbuschea** Sowerby, *Unio* : 1866, Conch. Iconica, **16**, *Unio*, pl. 51, species 269. (Hab. ?, Cuming colln.). BMNH [lost].
- vulcanus** Hanley, *Unio* : 1875, Proc. Zool. Soc. London, p. 606 (Birmah or Pegu). Holotype BMNH 1900.3.19.20, figured by Hanley and Theobald, 1876, Conch. Indica, p. 62, pl. 155, fig. 3.
- walpolei** Hanley, *Monocondylaea* : 1871, Proc. Zool. Soc. London, p. 587 (Sarawak, Borneo). Lectotype MCZ 175577, selected by Johnson 1948, Nautilus, **62** : 49, pl. 3, fig. 2 ; paralectotype BMNH 71.7.11.1, ex R. F. Geale.
- watersoni** Tomlin, *Anodonta* : 1923, Jour. of Conch., **17** : 68, text fig. (Lake Beschik, Salonika). Figured holotype BMNH 1923.12.31.95.
- welwitschii** Morelet, *Iridina* : 1868, Voyage dans les Royaumes d'Angola et de Benguella, p. 98 (la rivière Muria, près de Trombeta (Golungo-Alto) Angola). Lectotype, here selected, BMNH 93.2.4.1740, plate 1 fig. 1. Length 86, height 48, width 22 mm ; smaller paralectotype BMNH 93.2.4.1741.
- wolwichii** Morelet, *Unio* : 1845, Moll. de Portugal, p. 105, pl. 13, fig. 1 (les eaux de la vallée du Tage, entre Villa-Nova et Azumbuja [Portugal]). Holotype BMNH 93.2.4.1964 ; paratype BMNH 93.2.4.1965.
- woodthorpi** Godwin-Austen, *Margaritanopsis* : 1919, Records Indian Mus., Calcutta, **16** ; 204, pl. 14 (Fort Stedman, Shan States). Holotype BMNH 1965218 ; paratype BMNH 1965219.
- zambesiensis** Preston, *Unio* : 1905, Proc. Mal. Soc. London, **6** : 301, text fig. 1 (just above Victoria Falls, Zambesi River [Africa]). Figured holotype BMNH 1905.8.29.1.
- zonata** Hanley and Theobald, *Unio marginalis* : 1872, Conch. Indica, p. 20, pl. 44, fig. 2 (Belgaum, Deccan). Holotype BMNH 1907.10.28.252.

Part 2

FIGURED SPECIMENS OF UNIONACEA IN THE BRITISH MUSEUM (NAT. HIST.) WHICH ARE NOT TYPES

Material in square brackets indicates additional information, or more generally, that the locality was copied from the original description and does not necessarily apply to the specimen figured.

Specimens of Unionacea, exclusive of types, figured in : Reeve, L. and G. B. Sowerby, 1864-70, Conchologia Iconica, **16**, **17**.

1864-68, **16**, *Unio*.

- Pl. 1, fig. 1. *Unio boykinianus* Lea. [Chattahoochee River, Georgia and Warrior River, Alabama]. Cuming colln. BMNH 196473.
- Pl. 1, fig. 3. *Unio schoolcraftensis* Lea. [Fox River, Green Bay, Wisconsin, N. America]. Cuming colln. BMNH 196474.
- Pl. 1, fig. 4. *Unio verrucosus* Rafinesque. [River Ohio, N. America]. Cuming colln. BMNH 196475.
- Pl. 2, fig. 6. *Unio kleinianus* Lea. Suwanee River, Florida, North America. Cuming colln. BMNH 196476.
- Pl. 2, fig. 7. *Unio caelatus* Conrad. North America. Cuming colln. BMNH 196477.
- Pl. 3, fig. 10. *Unio turgidus* Lea. New Orleans, North America. Cuming colln. BMNH 196478.
- Pl. 3, fig. 11. *Unio apiculatus* Say. North America. Cuming colln. BMNH 196479.
- Pl. 4, fig. 14. *Unio sparsus* Lea. East Tennessee, North America. Cuming colln. BMNH 196480.
- Pl. 4, fig. 15. *Unio phillipsii* Conrad. North America. Cuming colln. BMNH 196481.
- Pl. 4, fig. 16. *Unio costatus* Rafinesque. North America. Cuming colln. BMNH 196482.
- Pl. 5, fig. 17. *Unio trapezoides* Lea. [Lake St. Joseph, Louisiana, North America]. Cuming colln. BMNH 196483.
- Pl. 5, fig. 20. *Unio elliotii* Lea. [Othcalooga Creek, Gordon County, Georgia, North America.]. Cuming colln. BMNH 196484.
- Pl. 6, fig. 22. *Unio flexuosus* Rafinesque. North America. Cuming colln. BMNH 196485.
- Pl. 6, fig. 24. *Unio quadratus* Rafinesque. Ohio River, North America. Cuming colln. BMNH 196486.
- Pl. 7, fig. 25. *Unio metanever* Rafinesque. North America. Cuming colln. BMNH 196487.
- Pl. 7, fig. 26. *Unio prasinus* Conrad. North America. Cuming colln. BMNH 196488 and 196489.
- Pl. 7, fig. 27. *Unio fragosus* Conrad. North America. Cuming colln. BMNH 196490.
- Pl. 8, fig. 28. *Unio cyphius* Rafinesque. North America. Cuming colln. BMNH 196491.
- Pl. 8, fig. 29. *Unio dromas* Lea. Tennessee, North America. Cuming colln. BMNH 196492.
- Pl. 9, fig. 32. *Unio nodulosus* Wood. [*Unio leaei* Gray (Errata)]. China. Cuming colln. BMNH 196493.
- Pl. 9, fig. 34. *Unio graniferus* Lea. Ohio River, North America. Cuming colln. BMNH 196494.
- Pl. 9, fig. 35. *Unio perplicatus* Conrad. North America. Cuming colln. BMNH 196495.
- Pl. 10, fig. 36. *Unio semigranosus* Philippi. Mexico. Cuming colln. BMNH 196496.
- Pl. 10, fig. 38. *Unio dorfeuillianus* Lea. Ohio River, North America. Cuming colln. BMNH 196497.
- Pl. 11, fig. 40. *Unio hippopaeus* Lea. Lake Erie, North America. Cuming colln. BMNH 196498.
- Pl. 11, figs. 41a, b. *Unio gibbosus* Rafinesque. North America. Cuming colln. a is BMNH 196499 ; b is BMNH 1964104.
- Pl. 11, fig. 42. *Unio perlensis* Conrad. North America. Cuming colln. BMNH 1964100.
- Pl. 12, fig. 43. *Unio bullatus* Rafinesque. North America. Cuming colln. BMNH 1964101.
- Pl. 12, fig. 45. *Unio stegarius* Rafinesque. North America. Cuming colln. BMNH 1964102.
- Pl. 12, fig. 46. *Unio pernodosus* Lea. North Carolina, North America. Cuming colln. BMNH 1964103.
- Pl. 13, fig. 47. *Unio nodiferus* Conrad. [North America]. Cuming colln. BMNH 1964105.
- Pl. 13, fig. 48. *Unio intermedius* Conrad. North America. Cuming colln. BMNH 1964106.
- Pl. 13, fig. 52. *Unio stapes* Lea. Alabama, North America. Cuming colln. BMNH 1964107.
- Pl. 14, fig. 54. *Unio rangianus* Lea. Ohio River, North America. Cuming colln. BMNH 1964108.
- Pl. 14, fig. 55. *Unio penitus* Conrad. Alabama, North America. Cuming colln. BMNH 1964109.

- Pl. 14, fig. 57. *Unio arcaeiformis* Lea. Tennessee River, North America. Cuming colln. BMNH 1964110.
- Pl. 14, fig. 58. *Unio sowerbyanus* Lea. Tennessee [River], North America. Cuming colln. BMNH 1964111.
- Pl. 14, fig. 59. *Unio pileus* Lea. Ohio River, North America. Cuming colln. BMNH 1964112.
- Pl. 14, fig. 60. *Unio sulcatus* Lea. Ohio River, North America. Cuming colln. BMNH 1964113.
- Pl. 15, fig. 62. *Unio haysianus* Lea. Cumberland River, North America. Cuming colln. BMNH 1964114.
- Pl. 15, fig. 63. *Unio ridibundus* Say. North America. Cuming colln. BMNH 1964115.
- Pl. 15, fig. 64. *Unio personatus* Say. Ohio River, North America. Cuming colln. BMNH 1964116.
- Pl. 15, fig. 65. *Unio edgarianus* Lea. Tennessee River, North America. Cuming colln. BMNH 1964117.
- Pl. 15, fig. 66. *Unio stewardsonii* Lea. Chattanooga River, North America. Cuming colln. BMNH 1964118.
- Pl. 16, fig. 68. *Unio nucleopsis* Conrad. North America. Cuming colln. BMNH 1964119.
- Pl. 16, fig. 69. *Unio chattanoogaensis* Lea. Chattanooga, [River] North America. Cuming colln. BMNH 1964120.
- Pl. 16, fig. 70. *Unio raveneliensis* Lea. Tennessee River, North America. Cuming colln. BMNH 1964121.
- Pl. 16, fig. 71. *Unio decusus* Lea. Alabama River, North America. Cuming colln. BMNH 1964122.
- Pl. 16, fig. 72. *Unio mundus* Lea. North America. Cuming colln. BMNH 1964123. [Not the *mundus* of Lea, but nearer his *mooresianus* and *cuneolus* (Errata)].
- Pl. 16, fig. 73. *Unio cuneatus* Rafinesque. North America. Cuming colln. BMNH 1964124.
- Pl. 16, fig. 74. *Unio woodwardianus* Lea. Georgia, North America. Cuming colln. BMNH 1964125.
- Pl. 17, fig. 75. *Unio lenior* Lea. Tennessee, North America. Cuming colln. BMNH 1964126.
- Pl. 17, fig. 77. *Unio medius* Lea. Alabama, North America. Cuming colln. BMNH 1964127.
- Pl. 17, fig. 78. *Unio subrostratus* Say. North America. Cuming colln. BMNH 1964128. [Nearer the *patulus* of Lea (Errata)].
- Pl. 17, fig. 79 a. *Unio capsaeformis* Lea. Cumberland River, North America. Cuming colln. BMNH 1964129.
- Pl. 18, fig. 92. *Unio perdix* Lea. Tennessee, North America. Cuming colln. BMNH 1964130.
- Pl. 18, fig. 84. *Unio obesus* Lea. [York River, Virginia] North America. Cuming colln. BMNH 1964131.
- Pl. 19, fig. 85. *Unio mississippiensis* Conrad, MS. Mississippi River, North America. Cuming colln. BMNH 1964132. Sent by Anthony to Cuming prior to publication in 1850.
- Pl. 19, fig. 86. *Unio rectus* Lamarck. North America. Cuming colln. BMNH 1964133.
- Pl. 19, fig. 87. *Unio anodontoides* Lea. North America. Cuming colln. BMNH 1964134.
- Pl. 20, fig. 88. *Unio buddianus* Lea. Florida, North America. Cuming colln. BMNH 1964135.
- Pl. 20, fig. 89. *Unio cucumoides* Lea. Hunter's River, New South Wales. Cuming colln. BMNH 1964136.
- Pl. 20, fig. 90. *Unio shepardianus* Lea. Georgia, North America. Cuming colln. BMNH 1964137.
- Pl. 21, fig. 93. *Unio patagonicus* d'Orbigny. Patagonia. Cuming colln. BMNH 1964138.
- Pl. 21, fig. 94. *Unio nasutus* Say. North America. Cuming colln. BMNH 1964139.
- Pl. 21, fig. 95. *Unio fuscatus* Lea. Florida, North America. Cuming colln. BMNH 1964140.
- Pl. 23, fig. 107. *Unio cuneolus* Lea. Tennessee, North America. Cuming colln. BMNH 1964142.
- Pl. 23, fig. 108. *Unio berlandierii* Lea. Mexico. Texas. Cuming colln. BMNH 1964143.
- Pl. 23, fig. 109. *Unio altilis* Conrad. North America. Cuming colln. BMNH 1964144.

- Pl. 24, fig. 113. *Unio fisherianus* Lea. [Chester River, Maryland, North America]. Cuming colln. BMNH 1964145.
- Pl. 24, fig. 114. *Unio navigioliiformis* Lea. Hab.? Cuming colln. BMNH 1964146.
- Pl. 24, fig. 115. *Unio purpuratus* Lamarck. Louisiana, North America. Cuming colln. BMNH 1964147.
- Pl. 24, fig. 116. *Unio haleianus* Lea. [Mississippi, near New Orleans, North America]. Cuming colln. BMNH 1964148.
- Pl. 25, fig. 119. *Unio grayanus* Lea. China. Cuming colln. BMNH 1964149.
- Pl. 25, fig. 125. *Unio verecundus* Gould. Manila, Island of Luzon, Philippines. Cuming colln. BMNH 1964150.
- Pl. 26, fig. 126. *Unio ingallsianus* Lea. [Siam ; Dr. Ingalls]. Cuming colln. BMNH 1964151.
- Pl. 26, fig. 127. *Unio incrassatus* Lea. Georgia, North America. Cuming colln. BMNH 1964152.
- Pl. 26, fig. 128. *Unio concestator* Lea. Georgia, North America. Cuming colln. BMNH 1964153.
- Pl. 26, fig. 129. *Unio obtusus* Lea. Georgia, North America. Cuming colln. BMNH 1964154.
- Pl. 26, fig. 132. *Unio aegyptiacus* Cailliaud. [River Nile, Egypt ; Cailliaud]. Cuming colln. BMNH 1964155.
- Pl. 27, fig. 133. *Unio solidus* Lea. [Ohio River, at Cincinnati, Ohio, North America]. Cuming colln. BMNH 1964156.
- Pl. 27, fig. 135. *Unio circulus* Lea. Ohio and Tennessee, North America. Cuming colln. BMNH 1964157.
- Pl. 27, fig. 139. *Unio radiatus* Gmelin. [Lake Georgia, North America]. Cuming colln. BMNH 1964158.
- Pl. 28, fig. 142. *Unio sumatrensis* Lea. Sumatra. Cuming colln. BMNH 1964159. This specimen was probably not seen by Lea. Holotype USNM 84059.
- Pl. 28, fig. 144. *Unio nitens* Lea. Tennessee, North America. Cuming colln. BMNH 1964160.
- Pl. 29, fig. 148. *Unio iris* Lea. Ohio. Cuming colln. BMNH 1964162.
- Pl. 29, fig. 149. *Unio contradens* Lea. River Mezherdeh, Tunis. Cuming colln. BMNH 1964163.
- Pl. 30, fig. 154. *Unio platyrhynchus* Rossmassler. Carinthia. Cuming colln. BMNH 1964164.
- Pl. 30, fig. 156. *Unio aucklandicus* Gray, Auckland, New Zealand, Cuming colln. BMNH 1964165.
- Pl. 31, fig. 162. *Unio ornatus* Conrad. Alabama. [Cuming colln.]. BMNH 1964166.
- Pl. 31, fig. 163. *Unio subovatus* Lea. Ohio. [Cuming colln.]. BMNH 1964167.
- Pl. 31, fig. 164. *Unio ovatus* Say. Ohio. [Cuming colln.]. BMNH 1964168.
- Pl. 32, fig. 165. *Unio negatus* Lea. [Big Prairie Creek, Alabama ; E. R. Showalter. Columbus ; Miss. ; Spillman]. Cuming colln. BMNH 1964169.
- Pl. 32, fig. 167. *Unio shuttleworthi* Lea. Australia ; Shuttleworth. Cuming colln. BMNH 1964170. Not seen by Lea, but mentioned by him as being in the Cuming colln. Holotype USNM 84416.
- Pl. 32, fig. 169. *Unio burroughianus* Lea. River Panama, South America. Cuming colln. BMNH 1964171.
- Pl. 33, fig. 170. *Unio umbrosus* Lea. [Medellin River, Mexico ; Dr. Burrough]. Cuming colln. BMNH 1964172.
- Pl. 33, fig. 171. *Unio medellinus* Lea. [River Medellin, near Vera Cruz ; Dr. Burrough. Cuming colln.]. BMNH 1964173.
- Pl. 33, fig. 172. *Unio hembeli* Conrad. Louisiana. Cuming colln. BMNH 1964174.
- Pl. 33, fig. 173. *Unio lecontianus* Lea. [River Georgia ; Major Leconte]. Cuming colln. BMNH 1964175.
- Pl. 34, fig. 175. *Unio buckleyi* Lea. [Lake George and Lake Munroe. Florida ; S. B. Buckley]. Cuming colln. BMNH 1964176.

- Pl. 34, fig. 176. *Unio discrepans* Lea. [North Alabama ; Prof. Tuomey]. Cuming colln. BMNH 1964177.
- Pl. 34, fig. 179. *Unio umbrans* Lea. [Othcalooga Creek, Gordon County, Georgia ; Bishop Elliot]. Cuming colln. BMNH 1964178.
- Pl. 34, fig. 180. *Unio barnesianus* Lea. [Cumberland River, Tennessee ; Dr. Troost]. Cuming colln. BMNH 1964179.
- Pl. 34, fig. 181. *Unio regularis* Lea. [French Broad River, East Tennessee ; Dr. Troost]. Cuming colln. BMNH 1964180.
- Pl. 35, fig. 182. *Unio micans* Lea. [Catawba River ; Wheatley. Deep River Gulf, North Carolina, Emmons. Cuming colln.]. BMNH 1964181.
- Pl. 35, fig. 183. *Unio pellucidus* Lea. [Chatahoochee River, Georgia]. Cuming colln. BMNH 1964182.
- Pl. 35, fig. 184. *Unio heterodon* Lea. Georgia. Cuming colln. BMNH 1964183.
- Pl. 35, fig. 185. *Unio confertus* Lea. South Carolina. Cuming colln. BMNH 1964184.
- Pl. 35, fig. 186. *Unio parvus* Barnes. [Fox River, North America]. Cuming colln. BMNH 1964185.
- Pl. 35, fig. 187. *Unio blandingianus* Lea. Florida. Cuming colln. BMNH 1964186.
- Pl. 35, fig. 188. *Unio haslehurstianus* Lea. [Satilla River, Camden County, Georgia ; C. T. Downie]. Cuming colln. BMNH 1964187.
- Pl. 36, fig. 189. *Unio acutissimus* Lea. Alabama River. Cuming colln. BMNH 1964188.
- Pl. 36, fig. 190. *Unio glans* Lea. River Ohio. [Cuming colln.]. BMNH 1964189.
- Pl. 36, fig. 191. *Unio zeiglerianus* Lea. Cumberland River, Tennessee. Cuming colln. BMNH 1964190.
- Pl. 36, fig. 192. *Unio hildrethianus* Lea. Ohio. Cuming colln. BMNH 1964191.
- Pl. 36, fig. 193. *Unio tortivus* Lea. [Chattahoochee River, Georgia]. Cuming colln. BMNH 1964192.
- Pl. 36, fig. 194. *Unio ahaeneus* Lea. [Black Creek, Florida]. Cuming colln. BMNH 1964193.
- Pl. 36, fig. 196. *Unio fabalis* Lea. [Ohio River ; Lea]. Cuming colln. BMNH 1964194.
- Pl. 36, fig. 197. *Unio cumberlandicus* Lea. Cumberland River. Cuming colln. BMNH 1964195.
- Pl. 37, fig. 200. *Unio lens* Lea. [River Ohio ; Lea. Tennessee ; Vanuxem]. Cuming colln. BMNH 1964196.
- Pl. 37, fig. 201. *Unio subrotundus* Lea. West Africa. [Cuming colln.]. BMNH 1964197.
- Pl. 37, fig. 202. *Unio foremanianus* Lea. Coosa River, Alabama. Cuming colln. BMNH 1964198.
- Pl. 37, fig. 203. *Unio hydeanis* Lea. [Teche River, Louisiana ; W. M. Stewart]. Cuming colln. BMNH 1964199.
- Pl. 37, fig. 204. *Unio argenteus* Lea. [Holston River, East Tennessee ; Dr. Troost]. Cuming colln. BMNH 1964200.
- Pl. 38, fig. 206. *Unio novi-eboraci* Lea. [Oak Orchard Creek, Orleans County, New York ; J.C. Jay]. Cuming colln. BMNH 1964201.
- Pl. 38, fig. 207. *Unio murchisonianus* Lea. [*Unio douglasiae* Gray (Errata)]. China. Cuming colln. BMNH 1964202.
- Pl. 38, fig. 208. *Unio exiguus* Lea. Chatahoochee River, Georgia. Cuming colln. BMNH 1964203. [Not so, possibly *fatuus* (Errata)].
- Pl. 38, fig. 210. *Unio troostensis* Lea. North America. Cuming colln. BMNH 1964204.
- Pl. 38, fig. 211. *Unio muhlfeldianus* Lea. Tennessee. Cuming colln. BMNH 1964205.
- Pl. 38, fig. 212. *Unio obesus* Lea. [York River]. Cuming colln. BMNH 1964206.
- Pl. 39, fig. 213. *Unio ziczac* Lea. South Carolina. Cuming colln. BMNH 1964207.
- Pl. 39, fig. 215. *Unio gracilis* Barnes. River Ohio. Cuming colln. BMNH 1964208.
- Pl. 39, fig. 216. *Unio vanuxemensis* Lea. River Cumberland, Tennessee. Cuming colln. BMNH 1964209.
- Pl. 39, fig. 217. *Unio stramineus* Conrad. River Alabama. Cuming colln. BMNH 1964210.

- Pl. 40, fig. 219. *Unio gibber* Lea. [Carryfork River, Tennessee ; Prof. Troost]. Cuming colln. BMNH 1964211.
- Pl. 40, fig. 220. *Unio crassus* Say. North America. Cuming colln. BMNH 1964212.
- Pl. 40, fig. 221. *Unio infucatus* Conrad. Georgia, America. Cuming colln. BMNH 1964213.
- Pl. 41, fig. 223. *Unio fibuloides* Lea. Connasuada River, Georgia. Cuming colln. BMNH 1964214.
- Pl. 41, fig. 226. *Unio caffer* Krauss [Is *U. africanus* Lea (Errata)]. Natal. Cuming colln. BMNH 1964215.
- Pl. 41, fig. 227. *Unio bigbyensis* Lea. Big Bigby Creek, Tennessee. Cuming colln. BMNH 1964216.
- Pl. 41, fig. 228. *Unio dolosus* Lea. Alabama River. Cuming colln. BMNH 1964217.
- Pl. 42, fig. 233b. *Unio lindsleyi* Lea. [Tennessee ; President Lindsley]. Cuming colln. BMNH 1964218.
- Pl. 43, fig. 237. *Unio delphinulus* Morelet. Yucatan. Hanley colln. BMNH 1917.10.28.182.
- Pl. 44, fig. 241. *Unio schwartzenbachii* Rossmassler [Bourguignat]. Hab.? Hanley colln. BMNH 1907.10.28.197.
- Pl. 47, fig. 253. *Unio greenii* Conrad. Virginia. Hanley colln. BMNH 1907.10.28.192.
- Pl. 47, fig. 254. *Unio hainesianus* Lea. Little Arkansas. Cuming colln. BMNH 1964219.
- Pl. 47, fig. 255. *Unio postellii* Lea. [Randall's Creek, near Columbia, Georgia]. Cuming colln. BMNH 1964220.
- Pl. 48, fig. 257. *Unio leptodon* Rafinesque. Hab. ?. Cuming colln. BMNH 1964354.
- Pl. 48, fig. 259. *Unio arcula* Lea. Georgia, in America. Cuming colln. BMNH 1964355.
- Pl. 48, fig. 260. *Unio housei* Lea. Georgia, in America. [Siam]. Cuming colln. BMNH 1964356.
- Pl. 49, fig. 261. *Unio spinosus* Lea. Georgia, in America. Cuming colln. BMNH 1964357.
- Pl. 49, fig. 262. *Unio crispisulcatus* Lea. [Benson (Errata)]. Hab? Cuming colln. BMNH 1964358.
- Pl. 49, fig. 263. *Unio collinus* Lea [Conrad]. Virginia. Cuming colln. BMNH 1964359.
- Pl. 50, fig. 265. *Unio myersianus* Lea. Camboja, Lao Mountains [Siam]. Cuming colln. BMNH 1964361.
- Pl. 50, fig. 266. *Unio complanatus* Barnes. Ohio. Cuming colln. BMNH 1964362.
- Pl. 51, fig. 267. *Unio marginatus* Lea. [Say] Massachusetts. Cuming colln. BMNH 1964363.
- Pl. 51, fig. 270. *Unio poulsoni* Conrad. Mississippi. Cuming colln. BMNH 1964364.
- Pl. 52, fig. 271. *Unio gravidus* Lea. Siam. Cuming colln. BMNH 1964365.
- Pl. 53, fig. 275. *Unio discoideus* Lea. Hab. ?. Cuming colln. BMNH 1964366.
- Pl. 53, fig. 276. *Unio nicklinianus* Lea. China. Cuming colln. BMNH 1964367.
- Pl. 54, fig. 277. *Unio percoarctatus* Lea. [Not so, approaches *laevissimus* Lea (Errata)]. Hab.? Cuming colln. BMNH 1964368.
- Pl. 56, fig. 284. *Unio decurvatus* Rossmassler. Germany. Taylor colln. BMNH 1874.12.11.14.
- Pl. 57, fig. 290. *Unio funebris* Lea. Uruguay, South America. Taylor colln. BMNH 1874.12.11.10.
- Pl. 57, fig. 291. *Unio tampicoensis* Lea. Tampico and Tecamate, in Mexico. Taylor colln. BMNH 1874.12.11.2
- Pl. 58, fig. 293 a, b. *Unio luteolus* Lamarck. Hab.? Taylor colln. a is BMNH 1874.12.11.18 ; b is BMNH 1874.12.11.19.
- Pl. 58, fig. 294. *Unio cariosus* Say. Hab. ?. Taylor colln. BMNH 1874.12.11.7.
- Pl. 59, fig. 296. *Unio congareus* Lea. Congaree River, Columbia [South Carolina]. Taylor colln. BMNH 1874.12.11.24.
- Pl. 59, fig. 297. *Unio marginalis* Lamarck. Bengal. Taylor colln. BMNH 1874.12.11.9.
- Pl. 59, fig. 298. *Unio dolabraeformis* Lea. Georgia. Taylor colln. BMNH 1874.12.11.6.
- Pl. 60, fig. 299. *Unio confragosus* Say. North America. Taylor colln. BMNH 1874.12.11.26.
- Pl. 60, fig. 301. *Unio jayensis* Lea. Hab.? Taylor colln. BMNH 1874.12.11.12.
- Pl. 60, fig. 302. *Unio rugosus* Barnes. North America. Taylor colln. BMNH 1874.12.11.20.

- Pl. 60, fig. 306. *Unio multiradiatus* Lea. [*Unio luteolus* var. (Errata)]. River Ohio. Taylor colln. BMNH 1874.12.11.28.
- Pl. 61, fig. 309. *Unio lineatus* Lea. [Chattahoochee River, Columbus, Georgia ; Dr. Boykin]. Taylor colln. BMNH 1874.12.11.27.
- Pl. 62, fig. 310. *Unio discus* Lea. India. [Habitat wrong (Errata)]. Sowerby colln. BMNH 1888.12.4.2016.
- Pl. 62, fig. 311. *Unio sinuatus* Lamarck. Rivers of Europe. Taylor colln. BMNH 1864.12.11.29.
- Pl. 63, fig. 317. *Unio ochraceus* Say. [Rivers Georgia, Schuylkill, Delaware, Savannah]. Taylor colln. BMNH 1874.12.11.5.
- Pl. 66, fig. 335. *Unio pullatus* Lea. River Georgia. Taylor colln. BMNH 1874.12.11.16.
- Pl. 67, fig. 339. *Unio wynegungensis* Lea. [Wynegunga River, Nagpoor, Bengal]. Taylor colln. BMNH 1874.12.11.8.
- Pl. 67, fig. 341. *Unio roanoakensis* Lea. Virginia. Taylor colln. 1874.12.11.21.
- Pl. 68, fig. 346. *Unio purpureus* Say. Massachusetts. Taylor colln. BMNH 1952.10.30.70.
- Pl. 68, fig. 349. *Unio hopetownensis* Lea. [Hopetown, Georgia]. Taylor colln. BMNH 1874.12.11.23.
- Pl. 68, fig. 350. *Unio downei* [sic] Lea. Hopetown, Georgia. Taylor colln. BMNH 1874.12.11.22.
- Pl. 69, fig. 353. *Unio osbeckii* Philippi. China. Taylor colln. BMNH 1874.12.11.13.
- Pl. 69, fig. 354. *Unio clava* Lamarck. Western waters in N. America. Hanley colln. BMNH 1952.10.30.69.
- Pl. 70, fig. 356. *Unio camptodon* Say. New Orleans, N. America. Hanley colln. BMNH 1952.10.30.68.
- Pl. 70, fig. 357. *Unio clairbornensis* Lea. [Alabama River, near Clairborne, N. America]. Hanley colln. BMNH 1952.10.30.71.
- Pl. 70, fig. 358. *Unio platyrrhinchoideus* Dupuy. Arcachon, Western France. Hanley colln. BMNH 1907.12.30.368.
- Pl. 70, fig. 359. *Unio powellii* Lea. [Saline River, Arkansas, N. America]. Hanley colln. BMNH 1952.10.30.57.
- Pl. 71, fig. 360. *Unio corrugatus* Chemnitz [Müller]. Coromandel, etc., East Indies. Hanley Colln. BMNH 1907.12.30.65.
- Pl. 71, fig. 361. *Unio forbesianus* Lea. Savannah River, North America. Hanley colln. BMNH 1907.10.28.200.
- Pl. 72, fig. 366. *Unio ravistellus* Morelet. Lake Ysabel, Guatemala. Hanley colln. BMNH 1907.12.30.379.
- Pl. 72, fig. 367. *Unio striatulus* Lea. Roanoke River, N. Carolina. U. States, N. America. Hanley colln. BMNH 1907.10.28.251.
- Pl. 72, fig. 369. *Unio rotundus* Spix. Brazil. Hanley colln. BMNH 1907.10.28.180.
- Pl. 72, fig. 370. *Unio subtentus* Say. S. Carolina, N. America. Hanley colln. BMNH 1907.12.30.313.
- Pl. 72, fig. 371. *Unio reniformis* Schmidt. [Rossmassler]. S. Germany. Hanley colln. BMNH 1907.12.20.371.
- Pl. 73, fig. 373. *Unio nux persica* Dunker. China. Hanley colln. BMNH 1907.10.28.174.
- Pl. 73, fig. 374. *Unio niloticus* Caillaud. The river Nile. Hanley colln. BMNH 1907.10.28.247.
- Pl. 73, fig. 378. *Unio phaseolus* Hildreth. River Wabash, etc., North America. Hanley colln. BMNH 1952.10.30.132.
- Pl. 73, fig. 379. *Unio gibbosus* Barnes. Upper Mississippi and Missouri, North America. Hanley colln. BMNH 1964.369.
- Pl. 74, fig. 381. *Unio variabilis* Maton. Rio de la Plata, S. America. Hanley colln. BMNH 1907.10.28.199.
- Pl. 74, fig. 382. *Unio ellipticus* Spix. Bahia, Brazil. Hanley colln. BMNH 1907.10.28.198.

- Pl. 74, fig. 383. *Unio oregonensis* Lea. Columbia River, Oregon. Hanley colln. BMNH 1907.12.30.52.
- Pl. 74, fig. 385. *Unio calamitarum* Morelet. Baluntíé, near Palenque. Hanley colln. BMNH 1907.12.30.377.
- Pl. 75, fig. 387. *Unio pliciferus* Lea. Mexico. Hanley colln. BMNH 1907.12.30.375.
- Pl. 75, fig. 389. *Unio teretiusculus* Philippi. Sennaar. Hanley colln. BMNH 1907.10.28.172.
- Pl. 75, fig. 391. *Unio famelicus* Gould. Walla Walla, Oregon, North America. Hanley colln. BMNH 1907.12.30.369.
- Pl. 75, fig. 392. *Unio capigliolo* Payraudeau. Corsica, etc. Hanley colln. BMNH 1952.10.30.133.
- Pl. 75, fig. 393. *Unio dehiscens* Say. Ohio. Hanley colln. BMNH 1907.12.30.370.
- Pl. 76, fig. 394. *Unio fabula* Lea. Cumberland River, Tennessee. Hanley colln. BMNH 1907.10.28.245.
- Pl. 76, fig. 397. *Unio elongatus* Lamarck. Europe. Hanley colln. BMNH 1907.12.30.345.
- Pl. 76, fig. 398. *Unio holstonianus* Lea. Holston River, U.S. North America. Hanley colln. BMNH 1907.12.30.372.
- Pl. 76, fig. 399. *Unio undulatus* Say. Massachusetts, etc., North America. Hanley colln. BMNH 1907.12.30.378.
- Pl. 77, fig. 401. *Unio corrianus* Lea. Pegu, (W. Theobald). Hanley colln. BMNH 1907.10.28.165.
- Pl. 77, fig. 402. *Unio kirtlandianus* Lea. Ohio, N. America. Hanley colln. BMNH 1907.10.28.177.
- Pl. 77, fig. 403. *Unio excavatus* Lea. Georgia and Alabama, N. America. Hanley colln. BMNH 1907.12.30.137.
- Pl. 78, fig. 406. *Unio troostensis* Lea. Cumberland River, N. America. Hanley colln. BMNH 1907.10.28.190.
- Pl. 78, fig. 407. *Unio striatus* Lea. Chattahoochie River, Columbus, Georgia, N. America. Hanley colln. BMNH 1907.12.30.57.
- Pl. 78, fig. 410. *Unio calceola* Lea. Ohio. Hanley colln. BMNH 1907.01.28.253.
- Pl. 78, fig. 411. *Unio corvus* Lea. Georgia, N. America. Hanley colln. BMNH 1907.10.28.186.
- Pl. 79, fig. 413 a. *Unio sandrii* Villa [Rossmassler]. Dalmatia. Hanley colln. BMNH 1952.10.30.135.
- Pl. 79, fig. 414. *Unio bonellii* Férussac [Rossmassler]. Illyria. Hanley colln. BMNH 1907.10.28.179.
- Pl. 80, fig. 418. *Unio fallax* Lea. Georgia and Tennessee, N. America. Hanley colln. BMNH 1907.10.28.191.
- Pl. 80, fig. 419. *Unio triangulata* Lea. Georgia, N. America. Hanley colln. BMNH 1907.10.28.246.
- Pl. 80, fig. 420. *Unio japanensis* Lea. Japan. Hanley colln. BMNH 1907.12.30.373.
- Pl. 80, fig. 423. *Unio lugubris* Lea. Hopeton, near Darien, N. America. Hanley colln. BMNH 1907.12.30.39.
- Pl. 85, fig. 450. *Unio asperatus* Lea. Alabama river, N. America. Hanley colln. BMNH 1907.10.28.160.
- Pl. 85, fig. 452. *Unio glaber* Lea. Tennessee, N. America. Hanley colln. BMNH 1907.12.30.55.
- Pl. 85, fig. 454. *Unio arctior* Lea. Ohio, near Cincinnati, N. America. Hanley colln. BMNH 1907.12.30.59.
- Pl. 85, fig. 455. *Unio multistriatus* Lea. Brazil. Hanley colln. BMNH 1907.10.28.196.
- Pl. 85, fig. 456. *Unio subovatus* Lea. Ohio. Hanley colln. BMNH 1907.10.28.167.
- Pl. 86, fig. 457. *Unio pellis-lacerti* Morelet. Siam. Hanley colln. BMNH 1907.10.29.248.
- Pl. 86, fig. 462. *Unio stonensis* Lea. Stones's River, Tennessee, America. Hanley colln. BMNH 1907.10.28.188.

- Pl. 86, fig. 463. *Unio hochstetteri* Dunker. [Lake Taupo, N. Zealand (*teste* Dunker)]. Hanley colln. BMNH 1907. 10.28.265.
- Pl. 87, fig. 466. *Unio fontaineanus* Orbigny. S. America. Hanley colln. BMNH 1907.10.28.163.
- Pl. 94, fig. 512. *Unio coccineus* Hildreth [Lea]. Ohio, N. America. BMNH 1907.10.28.238.
- Pl. 94, fig. 513. *Unio salweenianus* Gould. River Salween British Birmah. Hanley colln. BMNH 1907.10.28.189.
- Pl. 95, fig. 516. *Unio pugio* Benson. E. Indies. Hanley colln. BMNH 1907.10.28.257.
- Pl. 95, fig. 517. *Unio crebristriatus* Anthony. British Birmah, (Theobald). Hanley colln. BMNH 1907.12.30.42.
- Pl. 95, fig. 519. *Unio peguensis* Anthony. Pegu (Theobald). Hanley colln. BMNH 1907.10.28.259.
- Pl. 95, fig. 520. *Unio crassus* Say. N. America. Hanley colln. BMNH 1907.10.28.262. 1868, 16, *Mycetopus*.
- Pl. 1, fig. 1. *Mycetopus soleniformis* Orbigny. Bolivia. Cuming colln. BMNH 1963403.
- Pl. 2, fig. 6. *Mycetopus emarginatus* Lea. Siam. Cuming colln. BMNH 1964404. 1867-70, 17, *Anodon*.
- Pl. 5, fig. 11. *Anodon suborbiculatus* Say. River Oregon. Cuming colln. BMNH 1964371.
- Pl. 6, fig. 13. *Anodon gibba* [gibbum] Benson. River Kiang. Cuming colln. BMNH 1964372.
- Pl. 8, fig. 15, species 16. *Anodon sinuosus* Lamarck. Brazil. Cuming colln. BMNH 1964373.
- Pl. 8, fig. 18, species 19. *Anodon gigantea* Lea. Port Gibson. Cuming colln. BMNH 1964374.
- Pl. 9, fig. 21, species 22. *Anodon susannae* Griffiths. Rio de la Plata. Cuming colln. BMNH 1964375.
- Pl. 9, fig. 22, species 23. *Anodon wahlamatensis* Lea. Rio Sacramento, Wahlamat. Cuming colln. BMNH 1964377.
- Pl. 9, fig. 24. *Anodon gibbosus* Say. River Georgia. Cuming colln. BMNH 1964378.
- Pl. 12, fig. 36. *Anodon politus* [polita] Mousson. Siam. Cuming colln. BMNH 1964380.
- Pl. 12, fig. 37. *Anodon charpentieri* Küster. Hab.? Cuming colln. BMNH 1964381.
- Pl. 12, fig. 39. *Anodon obtusus* Spix. Brazil. Cuming colln. BMNH 1964382.
- Pl. 14, fig. 51. *Anodon ferussaciana* Lea. [Sciato [Scioto] River, near Columbus, Ohio]. Cuming colln. BMNH 1964383.
- Pl. 15, fig. 54. *Anodon oblongus* de Millet. D'Angere, Maine et Loire. Cuming colln. BMNH 1964385.
- Pl. 17, fig. 59. *Anodon incertus* Lea. River Ohio. Cuming colln. BMNH 1964386.
- Pl. 17, fig. 60. *Anodon edentulus* Lea. [Say]. North America. Cuming colln. BMNH 1964387.
- Pl. 17, fig. 61. *Anodon fragilis* Lamarck. River Ohio. Cuming colln. BMNH 1964388.
- Pl. 17, fig. 62. *Anodon newtonensis* Lea [Newtown Creek, New Jersey, near Philadelphia, Pennsylvania] Cuming colln. BMNH 1964389. Identified by Lea, but not a primary type.
- Pl. 17, fig. 64. *Anodon lucasii* Morelet [Deshayes]. Algeria. Cuming colln. BMNH 1964390.
- Pl. 18, fig. 69. [By Error]. *Anodon ferussaciana* Lea. Ponds near Montreal, [Canada]. Cuming colln. BMNH 1964391.
- Pl. 19, fig. 72. *Anodon rayi* Dupuy. Hab.? Cuming colln. BMNH 1964393.
- Pl. 19, fig. 73. *Anodon lacustris* Lea. Lakes in New York. Cuming colln. BMNH 1964394.
- Pl. 19, fig. 74. *Anodon salmonea* Lea. Ohio. Cuming colln. BMNH 1964395.
- Pl. 27, fig. 102. *Anodon imbecillis* Lea. Ohio River. Walpole colln. BMNH 1964396.
- Pl. 32, fig. 128. *Anodon pavonia* Lea. [Little Beaver, Ohio]. BMNH 1964399.
- Pl. 33, fig. 133. *Anodon stewartianus* Lea. [River Teche, Louisiana]. BMNH 1841.4.6.24. 1869, 17, *Hyria*.
- Pl. 3, fig. 6. *Hyria avicularis* Lamarck. Hab.? BMNH 1846.3.6.31.

Specimens of Unionacea, exclusive of types, figured in : Hanley, S., 1842-56, An Illustrated and Descriptive Catalogue of Recent Bivalve Shells, forming an appendix to the Index Testaceologicus.

Supplementary plates :

- Pl. 20, fig. 20. *Unio perdix* Lea. Tennessee. BMNH 1907.10.28.267.
- Pl. 20, fig. 21. *Unio hopetoniensis* Lea. Near Darien, [Georgia]. BMNH 1907.12.30.54.
- Pl. 20, fig. 22. *Unio cariosus* Say. N. America. BMNH 1952.10.30.62.
- Pl. 20, fig. 23. *Unio circulus* Lea. Ohio, etc. BMNH 1907.10.28.243.
- Pl. 20, fig. 26. *Unio undulatus* Barnes. Ohio. BMNH 1907.12.30.38.
- Pl. 20, fig. 27. *Unio tuberculatus* Barnes. N. America. BMNH 1907.10.28.162.
- Pl. 20, fig. 29. *Unio caelatus* Conrad. Tennessee. BMNH 1907.12.30.50.
- Pl. 20, fig. 32. *Unio pliciferus* Lea. Mexico. BMNH 1907.10.28.181.
- Pl. 20, fig. 33. *Unio semigranosus* Von dem Busch. Mexico. BMNH 1907.10.28.261.
- Pl. 20, fig. 36. *Unio tampicoensis* Lea. Mexico. BMNH 1907.10.28.268.
- Pl. 20, fig. 42. *Unio tenuissimus* Lea. Ohio. BMNH 1952.10.30.136.
- Pl. 20, fig. 44. *Unio delphinus* Gruner. Malacca. BMNH 1952.10.30.61.
- Pl. 20, fig. 48. *Unio ochraceus* Say. Delaware. BMNH 1907.10.28.166.
- Pl. 20, fig. 51. *Unio securis* Lea. Ohio. BMNH 1907.12.30.51.
- Pl. 20, fig. 53. *Unio marginalis* Lamarck. Bengal. BMNH 1952.10.30.65.
- Pl. 20, fig. 54. *Unio gibbosus* Barnes. N. America. BMNH 1907.12.30.34.
- Pl. 20, fig. 55. *Unio splendidus* Lea. Georgia in America. BMNH 1952.10.30.66.
- Pl. 20, fig. 56. *Unio egyptiacus* Cail. Egypt and Senegal. BMNH 1907.10.28.173.
- Pl. 20, fig. 57. *Unio collinus* Conrad. Virginia. BMNH 1907.12.30.60.
- Pl. 20, fig. 58. *Unio subrotundus* Lea. Ohio. BMNH 1907.10.28.195.
- Pl. 20, fig. 59. *Unio ravenelii* Lea. Tennessee. BMNH 1907.12.30.61.
- Pl. 21, fig. 1. *Unio cooperianus* Lea. Ohio. BMNH 1907.10.28.159.
- Pl. 21, fig. 2. *Unio orbiculatus* Hildreth. U. States. BMNH 1907.10.28.194.
- Pl. 21, fig. 3. *Unio paranensis* Lea. R. Parana. BMNH 1907.10.28.161.
- Pl. 21, fig. 4. *Unio lens* Lea. Ohio. BMNH 1907.10.28.171.
- Pl. 21, fig. 5. *Unio capsaeformis* Lea. N. America. BMNH 1907.10.28.241.
- Pl. 21, fig. 7. *Unio ellipsis* Lea. Ohio. BMNH 1907.10.28.242.
- Pl. 21, fig. 8. *Unio (Alasmodonta) rugosus* Barnes. N. America. BMNH 1907.12.30.367.
- Pl. 21, fig. 11. *Unio retusus* Lamarck. N. America. BMNH 1952.10.30.59.
- Pl. 21, fig. 13. *Unio littoralis* Lamarck. France, &c. BMNH 1907.10.28.158.
- Pl. 21, fig. 14. *Unio varicosus* Lea. Ohio. BMNH 1907.12.30.36.
- Pl. 21, fig. 22. *Unio pectorosus* Conrad. Tennessee. BMNH 1952.10.30.67.
- Pl. 21, fig. 24. *Unio verrucosus* Barnes. Hab.? BMNH 1907.10.28.164.
- Pl. 21, fig. 25. *Unio australis* Lamarck. New Holland. BMNH 1952.10.30.64.
- Pl. 21, fig. 29. *Unio auratus* Lea. N. America. BMNH 1907.12.30.148.
- Pl. 21, fig. 30. *Unio bilineatus* Benson. R. Hoogly, Hindostan. BMNH 1952.10.30.63.
- Pl. 21, fig. 35. *Unio triangularis* Barnes. North America. BMNH 1907.10.28.250.
- Pl. 21, fig. 37. *Unio iris* Lea. Ohio. BMNH 1907.10.28.193.
- Pl. 23, fig. 8. *Unio medellinus* Lea. Vera Cruz. BMNH 1907.10.28.184.
- Pl. 23, fig. 55. *Unio leaei* Gray Ohio, BMNH 1907.10.28.249.
- Pl. 23, fig. 56. *Unio spinosus* Lea. Georgia in America. BMNH 1907.12.30.37.
- Pl. 23, fig. 59. *Unio (Alasmodonta) bonellii* Férussac. S. Germany. BMNH 1907.10.28.168.
- Pl. 23, fig. 60. *Unio delphinulus* Morelet. Yucatan. BMNH 1952.10.30.134.
- Pl. 24, fig. 1. *Unio foliatus* Hildreth. United States. BMNH 1907.10.28.178.
- Pl. 24, fig. 2. *Unio haysianus* Lea. N. America. BMNH 1907.10.28.185.
- Pl. 24, fig. 3. *Unio hembeli* Conrad. Louisiana. BMNH 1907.12.30.35.
- Pl. 24, fig. 4. *Unio cucumoides* Lea. Australia. BMNH 1907.10.28.244.
- Pl. 24, fig. 5. *Unio grayanus* Lea. China. BMNH 1907.10.28.170.
- Pl. 24, fig. 8. *Unio ventricosus* Barnes. North America. BMNH 1907.10.28.256.
- Pl. 24, fig. 10. *Unio (Margaritana) curreyanus* Lea. Tennessee. BMNH 1907.10.28.266.

- Pl. 24, fig. 13. *Anodonta wahlamatensis* Lea. Near the Rocky Mountains. BMNH 1907.12.30.33.
 Pl. 24, fig. 15. *Anodonta angulata* Lea. California. BMNH 1907.12.30.32.
 Pl. 24, fig. 17. *Anodonta ensiformis* Spix. Brazil. BMNH 1907.12.30.156.
 Pl. 24, fig. 18. *Anodonta blainvilliana* Lee. Chili? [on plate caption, spelled *blainvilleana*].
 BMNH 1908.12.15.19.

Specimens of Unionacea, exclusive of types, figured in : Hanley, S., 1863, Photographic Conchology, a second, or photographic series of the Conchological Miscellany & c. pp. 3 : 7 photo pls. col. 4to. London.

No localities are given in this work, the localities are from the boxes in which the specimens were found.

- Pl. 1, fig. 2. *Anodonta ferruginea* Lea. [Indiana]. BMNH 1908.12.15.15.
 Pl. 1, fig. 3. *Anodonta subcrassa* Lea. [Phillippine Is]. BMNH 1908.12.15.11.
 Pl. 1, fig. 5. *Anodonta ferussacciana* Lea. [Ohio]. BMNH 1908.12.15.10.
 Pl. 1, fig. 6. *Anodonta cumingii* Lea. BMNH 1908.12.15.1.
 Pl. 1, fig. 9. *Anodonta pavonia* Lea. [Ohio]. BMNH 1908.12.15.17.
 Pl. 2, fig. 1. *Unio menziesii* Gray. [New Zealand]. BMNH 1908.12.15.5.
 Pl. 2, fig. 2. *Unio decurvatus* Rossmassler [Germany]. BMNH 1908.12.15.3.
 Pl. 2, fig. 9. *Unio tirostris*. [Hindustan] BMNH 1907.12.30.45.
 Pl. 2, fig. 10. *Unio prevostianus* Lea. [Georgia]. BMNH 1908.12.15.18.
 Pl. 3, fig. 2. *Unio lineatus* Lea. [Georgia]. BMNH 1908.12.15.7.
 Pl. 3, fig. 4. *Unio boykinianus* Lea. [Alabama]. BMNH 1908.12.15.16.
 Pl. 4, fig. 1. *Unio bigbyensis* Lea. [Tennessee]. BMNH 1908.12.15.2.
 Pl. 4, fig. 2. *Unio crocodilorum* Morelet. [Central America]. BMNH 1908.12.15.4.
 Pl. 4, fig. 5. *Unio preovalis* Conrad. [Alabama]. BMNH 1908.12.15.6.
 Pl. 4, fig. 8. *Unio spatulatus* Lea. [Wisconsin]. BMNH 1908.12.15.14.
 Pl. 5, fig. 1. *Anodonta rubens* Lamarck. [Lower Nile]. BMNH 1908.12.15.8.
 Pl. 5, fig. 2. *Mycetopus siliquosus* Spix. [Panama River]. BMNH 1908.12.15.12.
 Pl. 5, fig. 4. *Unio (Symphonata) cumingii* Lea. [Alabama]. BMNH 1908.12.15.9.

Specimen of Unionidae figured in ; Forbes, E. and S. Hanley, 1853, A History of British Mollusca and Their Shells.

- Pl. 40, fig. 3. *Anodonta cygnea* Linnaeus. BMNH 1907.12.30.53.

Specimens of Unionacea, exclusive of types, figured in : Hanley, S. and W. Theobald, 1870-76. Conchologia Indica ; Illustrations of the Land and Freshwater Shells of British India.

- Pl. 9, fig. 3. *Trigonodon crebristriatum* Anthony. British Birmah. BMNH 1907.10.28.204.
 Pl. 9, fig. 4. *Pseudodon salweenianum* Gould. Salween River, Birmah. BMNH 1907.12.30.44.
 Pl. 9, fig. 5. *Trigonodon crebristriatus*, var. Anthony. Hab.? BMNH 1907.10.28.203.
 Pl. 9, fig. 6. *Unio lamellatus* [generosus on box], var. Lea. A peculiar winged form from Mandalay. BMNH 1907.10.28.254.
 Pl. 10, fig. 1. *Unio olivarius* Lea. Rohilcund Streams. BMNH 1907.12.30.62.
 Pl. 10, fig. 4. *Unio macilentus* Benson. "Bengal", Mandalay. BMNH 1907.12.30.41.
 Pl. 10, fig. 6. *Unio bonneaudi* Eydoux and Souleyet. Bhama, [Bhamdo] Upper Birmah (Blanford). BMNH *415.06.1.1.
 Pl. 10, fig. 7. *Unio pugio* Benson. Ava. Pegu (Theobald). BMNH 1907.10.28.258.
 Pl. 11, fig. 1a. *Unio favidens* Benson. Sunderbund, Bengal. BMNH 1907.12.30.43.
 Pl. 11, fig. 5. *Unio crispisulcatus* Benson. Tenasserim ; Pegu. BMNH 1907.10.28.263.
 Pl. 11, fig. 9. *Unio tirostris* Benson. non Reeve 1868. Moradabad. BMNH 1907.12.30.47.
 Pl. 12, fig. 2. *Unio gerbidoni* Eydoux and Souleyet. "Coromandel". BMNH *418.06.1.1.
 Pl. 12, fig. 3, 3a. *Unio caeruleus* Lea. River Hooghly, &c. BMNH 1907.12.30.63.
 Pl. 12, fig. 4. *Unio gerbidoni*, var. Eydoux and Souleyet. Hab.? BMNH 1907.12.30.67.

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- Pl. 12, fig. 6a. *Unio leioma* Benson. Near Bombay. BMNH 1907.12.30.66.
 Pl. 42, fig. 1. *Unio birmanus* Blanford. Bhamo, Upper Birmah. BMNH *551.06.1.1.
 Pl. 42, fig. 3. *Unio foliaceus* Gould. Tavoy, Birmah, Pegu. BMNH 1907.10.28.240.
 Pl. 42, figs. 5, 6. *Unio marcens* Hanley (for *U. favidens*, var. *marcens* of Benson). Berhampooter River, Assam. BMNH *424.06.1.1.
 Pl. 42, fig. 7. *Unio marginalis*, var. *anodontina* Küster (*U. anodontinus*, Küster non Lamarck). River Godavery ; Nagpoor ; Sylhet. BMNH *451.06.1.1.
 Pl. 43, fig. 4. *Unio marginalis* var. *candaharica* Hutton. River Sutlej. BMNH 1907.10.28.176.
 Pl. 44, fig. 4. *Unio marginalis*, var. *corriana* Lea (*U. corrianus* Lea). Near Calcutta &c. BMNH 1907.10.28.187.
 Pl. 44, figs. 5, 6. *Unio corrugatus*, var. *laevirostris* Benson (*U. laevirostris* Benson). River Godavery ; Penguang &c. BMNH 1907.10.28.260.
 Pl. 45, fig. 2. *Unio corrugatus* Müller, var. *solida*. From the River Godavery. BMNH *420.06.1.1.
 Pl. 45, fig. 3. *Unio corrugatus* Lea. Nagpoor ; Pengunga. BMNH *603.06.1.1.
 Pl. 45, fig. 6. *Unio wynegungaensis* Lea. River Wynegunga, &c. BMNH 1907.12.30.58.
 Pl. 46, fig. 3. *Unio scobina*?, var. Benson. Belgaum, Deccan. BMNH *515.06.1.1.
 Pl. 107, fig. 2. *Unio triembolus* Benson. Nerbudda River. BMNH *493.06.1.1.
 Pl. 107, fig. 4. *Unio indicus*, var. *aurea* Sowerby. Nerbudda River. BMNH 1907.12.30.40.
 Pl. 107, figs. 6, 7. *Unio sikkimensis* Lea. Assam. BMNH *2416.03.viii.1.
 Pl. 154, fig. 2. *Unio parma*?, var. Benson. Bhamao. BMNH *617.06.1.1.
 Pl. 154, fig. 3. *Unio rugosus* Gmelin. Coromandel. BMNH 1907.12.30.64.
 Pl. 154, fig. 4. *Unio mandelyayanus* Theobald. Mandelay, Birmah. BMNH 1907.12.30.49.
 Pl. 154, fig. 5. *Unio macilentis*, var. Surat. Near Chimoor ; Pem Gunga. BMNH *622.06.1.1.
 Pl. 154, fig. 7. *Unio tavoyensis*?, var. ; Birmah. BMNH 1907.12.30.376.
 Pl. 155, fig. 2. *Unio bhamaoensis* Theobald. Near Bhamae, and from Western Prome, Pegu. BMNH 1907.10.28.169.

* Goodwin-Austen's catalogue number.



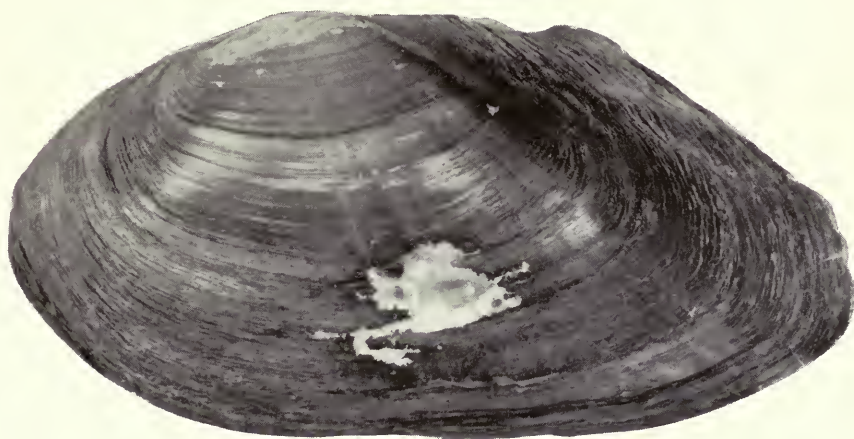
PLATE I

- FIG. 1. *Iridina welwitschii* Morelet. La rivière Muria, prés de Trombeta (Golungo-Alto) Angola. Lectotype BMNH 93.2.4.1740. Length 86, height 48, width 22 mm.
- FIG. 2. *Anodon lucasii* Morelet. La Calle [Algeria]. Holotype BMNH 93.2.4.1950. Length 107, height 56, width 33 mm.
- FIG. 3. *Spatha baikii* A. Adams. River Niger [Nigeria]. Lectotype BMNH 196466. Length 116, height 75, width 46 mm.

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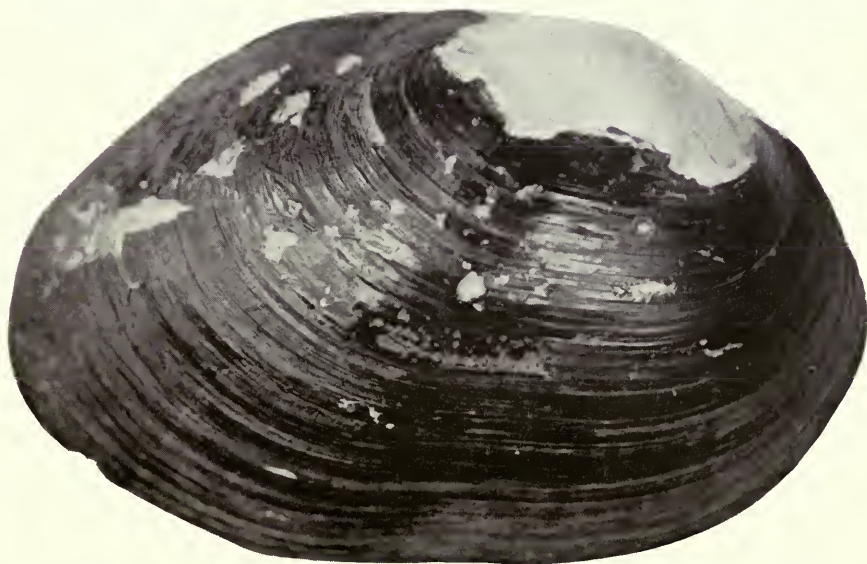


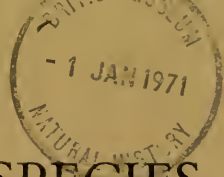
PLATE 2

- FIG. 1. *Unio episcopalis* Tristram. Orontes River, Palestine. Lectotype BMNH 1936.3.10.3
Length 80, height 47, width 28 mm.
- FIG. 2. *Unio simonis* Tristram. Orontes River, Palestine. Holotype BMNH 1936.3.10.6.
Length 48, height 35, width 24 mm.
- FIG. 3. *Unio scammatus* Morelet. Rio Tacataco [Pinar del Rio] Cuba. Lectotype BMNH 1893.
2.4.1976. Length 52, height 34, width 17 mm.
- FIG. 4. *Anodonta tunizana* Morelet. (La Calle), Tuniza. Lectotype BMNH 1893.2.4.1964.
Length 55, height 32, width 20 mm.
- FIG. 5. *Unio calamitarum* Morelet. Rivulum Baluntie, propré Palenqueanum vicum [Chiapas,
Mexico]. Lectotype BMNH 1893.2.4.2010. Length 54, height 32, width 26 mm.
- FIG. 6. *Unio sitifensis* Morelet. L'oued dehhab, près d'Bone, Algeria. BMNH 1893.2.4.1965.
Length 71, height 33, width 23 mm.



Printed in Great Britain by
Alden & Mowbray Ltd
at the Alden Press, Oxford

S. 1371: 2



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BUDDE-LUND, 1885 (ISOPODA,
PORCELLIONIDAE)

R. J. LINCOLN

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BY
ROGER JOHN LINCOLN

Xref

Pp. 109-130 ; 8 Text-figures

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THE BULLETIN OF THE BRITISH MUSEUM
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of the Museum, and an Historical series.*

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series. The abbreviated titles of periodicals cited
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*World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).*

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 10 December, 1970

Price 80 p

A REVIEW OF THE SPECIES OF *HEMILEPISTUS* S. STR. BUDDE-LUND, 1885 (ISOPODA, PORCELLIONIDAE)

By R. J. LINCOLN

SYNOPSIS

A brief historical review of relevant literature is given. At the present time the genus *Hemilepistus* is divided into two sub-genera, *Desertellio* and *Hemilepistus* sensu-stricto. The latter group is dealt with in this paper. The sub-genus *Hemilepistus* contains nine recognised species, with a range of distribution from North Africa, through the Near Eastern countries, into central Asia. A diagnosis, with figures, is given for each species, together with a key for their identification. Details of distribution are provided in each case. The synonymy for each species is presented. Where possible type material has been studied, and the locations of the types are indicated in the lists of material examined.

INTRODUCTION

BUDDE-LUND (1879) proposed the division of the genus *Porcellio* Latreille into seven sub-genera, but did not give any descriptive details of these divisions until the publication of his monograph on terrestrial isopods in 1885. As erected by Budde-Lund, the sub-genus *Hemilepistus* contained 10 species, of which 4 were newly described.

The earliest description of a terrestrial isopod which can be attributed to *Hemilepistus* is found in an account of a journey through Russia by Pallas (1771). Further species are contained in the beautifully illustrated account of the fauna of Egypt compiled by Audouin and Savigny (1826), and amongst the crustacean fauna of Turkestan described by Uljanin (1875). Brandt (1833) and Milne-Edwards (1840) published lists of the species of *Porcellio* known at that time, and included a number of new species which were later placed under *Hemilepistus*.

Budde-Lund (1885) split the species of *Hemilepistus* into two groups, each of 5 species, on the basis of the presence or absence of a median frontal line between the frons and the epistome. Verhoeff (1930) used this character to erect two new sub-genera, *Hemilepistus* and *Desertellio*. This raised *Hemilepistus* Budde-Lund to generic status, a move which appears to have been adopted much earlier by Budde-Lund and Stebbing (1911). In a subsequent account of isopods from the Mediterranean coasts, Verhoeff (1931) describes two new species of *Hemilepistus*, but he makes no mention of the sub-genera which had been proposed. Arcangeli (1932) considers a number of the species of *Hemilepistus* to be invalid and arrives at a lengthy synonymy under *crenulatus* Pallas.

More recently some Russian zoologists have made studies of this group of terrestrial isopods with a special interest in their biology and ecology. Borutzky (1945) gives a description of the woodlice fauna of Turkmeniya and central Asia, and produces

the first key for identification of the species of that area. He adopts the sub-genera of Verhoeff, and adds a further five new species. In a subsequent paper on *Hemilepistus*, Borutzky (1958) gives another key and drawings of a number of species. However, this account differs in many respects from the earlier paper and indicates Borutzky's uncertainty about the validity of some members of the genus.

In undertaking this review of the sub-genus *Hemilepistus* s. str. the type material has been examined wherever possible. Much of the Budde-Lund collection is held in the British Museum (Natural History), together with a number of the Verhoeff syntypes. The location of other type material is given in the relevant parts of the text.

Hemilepistus Budde-Lund, 1879

Body long, convex, grey or greyish-brown in colour with lighter tuberosity ; head and anterior peraeon tergites with armature of conical tubercles, which may be small and rounded or developed into large prominent crests ; lateral lobes on head small and set at an oblique angle ; eyes large, convex ; median frontal lobe on head small or absent ; pleon small, narrower than peraeon, smooth dorsally ; telson triangular with rounded apex ; antenna 2 short, with strongly developed peduncle and small, two segmented flagellum ; exopods of pleopods large, expanded ; 2-5 prs of pseudo-tracheae.

KEY TO THE SUB-GENERA OF *Hemilepistus*

- | | | |
|---|---|-----------------------------|
| 1 | Frontal median lobe of head absent | <i>Hemilepistus</i> s. str. |
| 2 | Frontal median lobe present, either entire or cleaved in the centre | <i>Desertellio</i> Verhoeff |

Hemilepistus (Hemilepistus) Budde-Lund, 1879

Body elongate, slate grey or brown with tubercles lighter in colour ; head with well defined pattern of conical tubercles on dorsal side, sometimes a number of additional smaller tubercles within basic arrangement ; lateral lobes of head oblique with small projecting upper lobes ; median lobe and suture line absent ; peraeon tergites 1-3 with well developed tubercles along posterior and lateral margins ; tubercles may form prominent crests ; (arrangement of tubercles on lateral and posterior margins of tergites 1-3 is expressed numerically as the " Dental formula ") ; peraeon tergites 4-7 smooth ; peraeon tergite 1 with prominent antero-lateral projection of epimera, apex pointed or acutely rounded ; pleon short, smooth, and with pointed, backwardly directed, epimera ; telson triangular, usually with slight dorsal depression, margins either straight or concave ; antenna 1 very small ; antenna 2 short, reaching only as far as posterior edge of peraeon tergite 1, peduncle strongly developed, segment 2 usually with prominent inner lobe, segment 5 elongate ; flagellum markedly shorter than last segment of peduncle ; flagellum segments either sub-equal, or segment 1 longer than segment 2 ; mandible large, 4-7 penicilli (fig. 1*k*) ; maxilla 2 small, bilobed (fig. 1*l*) ; maxilla 1 and maxillipeds strongly developed (figs. 1*i*, *j*) ; peraeopod 1, ♂ (fig. 1*b*) small, basis long, merus and carpus with long spines ; peraeopod

7, ♂ (fig. 1a) large, with elongate segments and prominent spines; exopods of pleopods 1-5 (figs. 1c-g) large, expanded and with pseudotracheae; pseudotracheae on exopods 1-2 large, 3 small, 4-5 rudimentary; uropods short, conical (fig. 1h); body size, length 10-30 mm, width 4.0-10.5 mm.

At the present time there are 9 species recognised within the sub-genus *Hemilepistus* s. str.

1. *H. (H.) klugii* (Brandt, 1833)
2. *H. (H.) crenulatus* (Pallas, 1771)
3. *H. (H.) reaumuri* (Audouin & Savigny, 1826)
4. *H. (H.) cristatus* Budde-Lund, 1879
5. *H. (H.) magnus* Borutzky, 1945
6. *H. (H.) reductus* Borutzky, 1945
7. *H. (H.) rhinoceros* Borutzky, 1958
8. *H. (H.) aphganicus* Borutzky, 1958
9. *H. (H.) schirasi* n. sp.

An important taxonomic character for the separation of the species is the arrangement of tubercles on the head and peraeon tergites. Although this is a satisfactory criterion, care must be exercised when attempting to identify a particular specimen as the degree of development of the tubercles varies with the size of the animal. The peraeon tubercles can be small and conical, or they may be much larger and form tall, comb-like crests. The shape of the telson also varies with the size of the individual. The juvenile form is usually a regular triangle, taking on the adult shape as the size of the animal increases.

Budde-Lund describes one of his species—*pectinatus*, from a single female specimen, making special reference to a marked suture line between the tergites and epimera of peraeon segments 2-4. Omer-Cooper (1923) remarks upon the same feature in a collection of female *Hemilepistus* from Mesopotamia, and places them in *pectinatus* Budde-Lund. However, Tait (1916) has pointed out that these suture lines do in fact appear in the cuticle of terrestrial isopods over a short period during a moult. Examination of the *Hemilepistus* material has revealed suture lines in several species including *klugii*, *crenulatus*, *reaumuri* and *aphganicus*.

1. *Hemilepistus (H.) klugii* (Brandt, 1833)

(text-figs. 1a-l, 2a-e)

Porcellio klugii Brandt, 1833 : 179; Milne-Edwards, 1840 : 171.

Hemilepistus klugii; Budde-Lund, 1879 : 4; 1885 (part) : 152; Borutzky, 1951 : 162, fig. 1; 1958 : 1464, fig. 2.

Hemilepistus crenulatus; Arcangeli, 1932 (part) : 1.

MATERIAL EXAMINED. 1 ♂, length 18 mm, width 6.5 mm. Syntype, collected by Olivier in the region of the Caucasus. Berlin Museum, cat. no. 7083.

1 ♂, 1 ♀, length 19-20 mm, width 7.0-7.5 mm. Budde-Lund collection from Tehran. B.M. (N.H.), reg. no. 1921.10.18, 4110-4111.

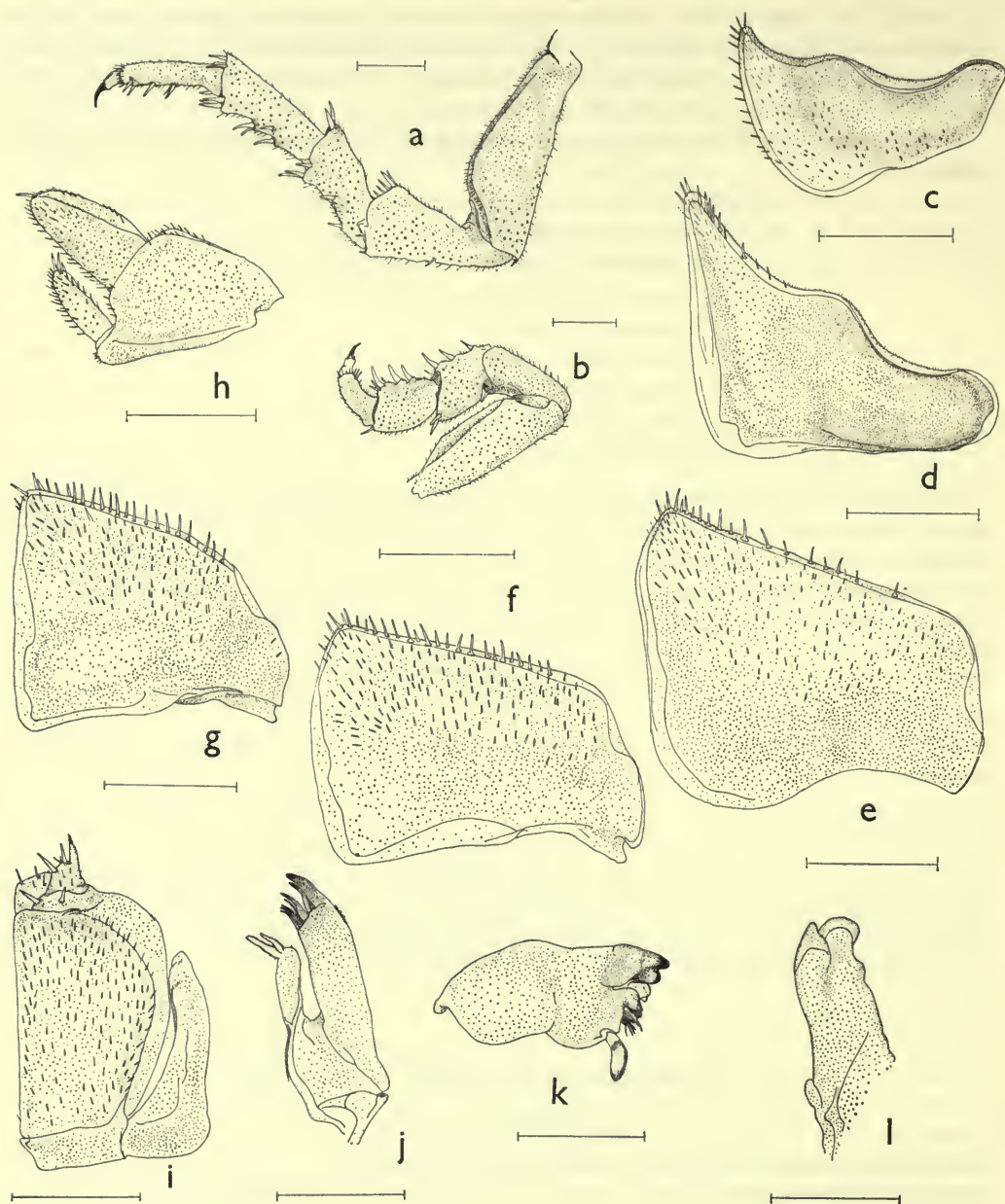


FIG. 1. *Hemilepistus klugii* (Brandt) ; *a*, 7th pereopod (left) ; *b*, 1st pereopod (left) ; *c-g*, exopods of pleopods 1-5 (left) ; *h*, uropod (left) ; *i*, maxilliped (left) ; *j*, maxilla 1 (left) ; *k*, mandible (right) ; *l*, maxilla 2 (left) ; bar scale 1 mm.

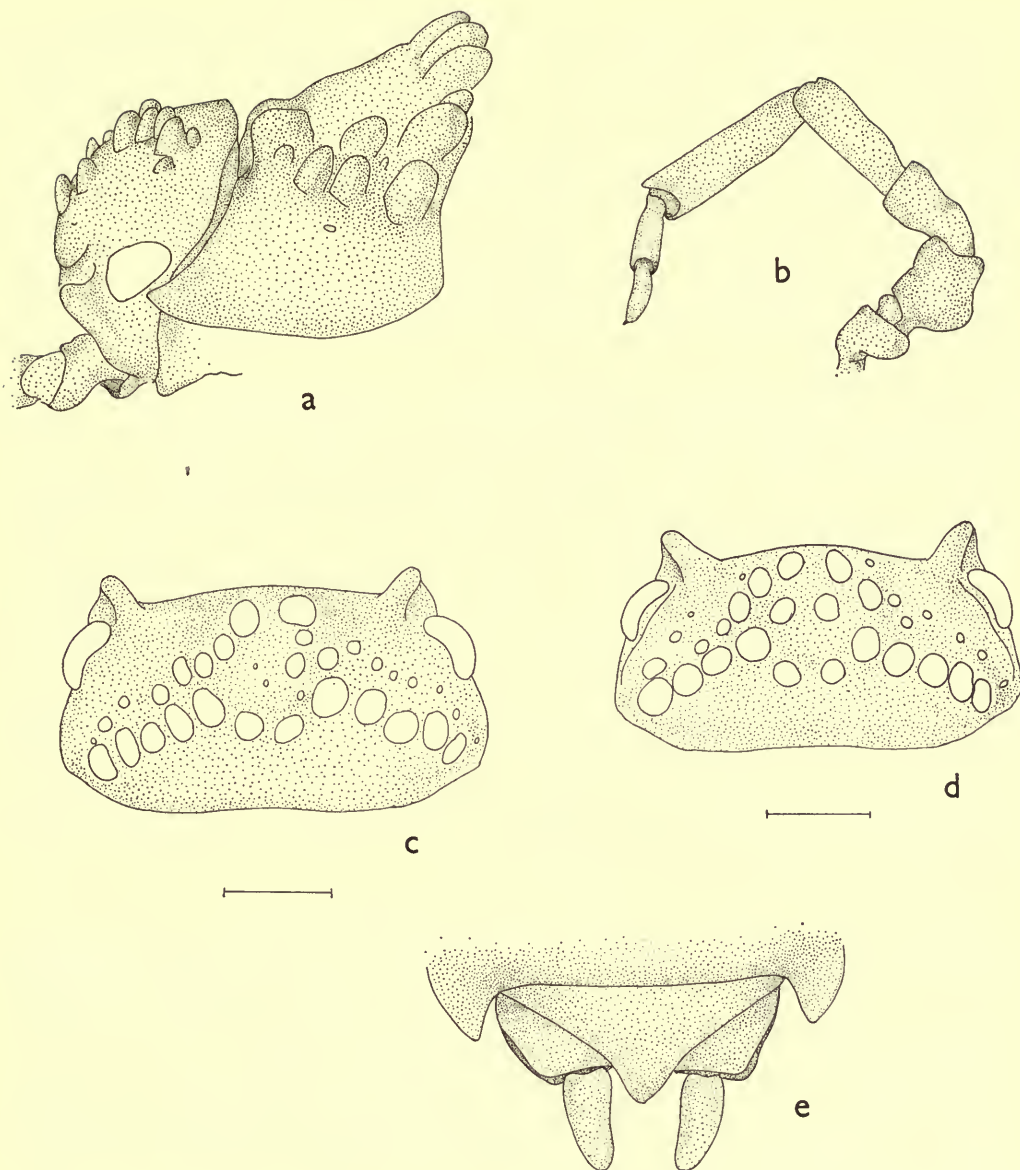


FIG. 2. *Hemilepistus klugii* (Brandt) ; a, lateral view of head and tergite 1 ; b, antenna 2 ; c, dorsal view of head (Syntype) ; d, dorsal view of head ; e, telson ; bar scale 1 mm.

1 ♂, 2 ♀♀, length 14–20 mm, width 5.5–7.5 mm. Budde-Lund collection from the Caucasus. B.M. (N.H.), reg. no. 1921.10.18, 4106–4109.

1 ♂, 1 ♀ (3 juveniles), length 13–15 mm, width 4.5–5.0 mm. Budde-Lund material, collected by Walter in Ashkhabad. B.M. (N.H.), reg. no. 1921.10.18, 4097–4101.

4 ♂♂, 6 ♀♀, length 14–19 mm, width 5.5–7.5 mm. Collected in the Caucasus. Leningrad Museum. Cat. no. 1677.

DIAGNOSIS. Body broad, length 13–20 mm, width 4.5–7.5 mm, greyish-brown with tubercles and epimera paler in colour; peraeon somewhat rectangular, tergites 5–7 slightly broader than rest; head with 16–20 rounded tubercles in a characteristic pattern over a triangular area; pattern consists of large circle in middle of head with lateral rows of 3–4 tubercles extending to postero-lateral corners (fig. 2c, d); sometimes 1–2 tubercles in centre of the large circle and a number of smaller tubercles within the triangular area; head with prominent lateral lobes, upper part of lobes rounded, outer edges sinuous (fig. 2a); ratio of width of head to width of peraeon tergite 2 is about 1 : 1.8; peraeon tergite 1, antero-lateral projection of epimera short, only slightly upturned and with rounded apex (fig. 2a); peraeon tergites 1–3 with short, conical tubercles along posterior and lateral margins; outer tubercles along posterior margin more bulbous than inner ones, those on tergite 1 set at right angles to dorsal surface; posterior edge of tergite 1 strongly developed; tubercles on tergites 2–3 projecting backwards parallel to dorsal surface; peraeon lateral tubercles prominent, anterior tubercle on tergite 1 largest, flattened and rectangular; tergite 4 with only faint traces of tuberosity; tergites 5–7 smooth; (dental formula, tergite 1, 3–4, 14, 3–4; tergites 2 & 3, 2–3, 14, 2–3); in large specimens tubercles on tergites 1–3 may form prominent crests; telson triangular with shallow dorsal depression, lateral margins concave (fig. 2e); antenna 2, peduncle segment 2 with large inner lobe, flagellum about $\frac{2}{3}$ length of peduncle segment 5, flagellum segment 1 longer than 2 (fig. 2b); mandibles (fig. 1k), maxillules (fig. 1j), maxillae (fig. 1l), maxillipeds (fig. 1i), peraeopods 1 (fig. 1a), and peraeopods 2 (fig. 1b), as figured; exopods of pleopods 1–5 ♂ (fig. 1c–g), pseudotracheae on pleopods 1–2 very well developed, small on 3 and rudimentary on 4–5; exopods of pleopod 1 ♂, with strongly sinuous posterior margin and prominent rounded inner angle (fig. 1c).

DISTRIBUTION. Caucasus; Apsheron peninsular; northern Iran.

REMARKS. Budde-Lund (1885) gives two separate localities for the distribution of *klugii*. The first is "Caucasus" from material in the Berlin Museum, and the second is "Schiras in Persia" based upon three specimens in the Copenhagen Museum. Both of these collections have been examined and it is clear that they represent quite different species. The material from the region of the Caucasus is the true *klugii*. The other specimens from Iran will be described later as a new species. Borutzky (1958) was the first to place doubt on the validity of the Budde-Lund *klugii* from Schiras and included it in a list of species of uncertain taxonomic position, but without giving any reasons.

2. *Hemilepistus (H.) crenulatus* (Pallas, 1771)

(text-figs. 3a–h)

Oniscus crenulatus Pallas, 1771 : 477.

Porcellio crenulatus; Latreille, 1804 : 46.

Porcellio elegans Uljanin, 1875 : 6.

Hemilepistus elegans ; Budde-Lund, 1879 : 4 ; 1885 : 154 ; Borutzky, 1945 : 195.

Hemilepistus crenulatus ; Budde-Lund, 1885 : 153 ; Arcangeli, 1932 (part) : 1 ; Borutzky, 1958 : 1465.

Hemilepistus pectinatus Budde-Lund, 1885 : 153 ; Borutzky, 1945 : 195 ; 1958 : 1467.

MATERIAL EXAMINED. 2 ♂♂, length 14 mm, width 4.5 mm. Syntypes of *elegans* Uljanin, collected in valley of Syr-darya, Turkestan. Berlin Museum, cat. no. 6630 (figs. 3*b*, *d*, *g*).

1 ♂, (1 juvenile), length 16.5 mm, width 5.0 mm, collected by Dr. Pawlowsky in Turkestan. B.M. (N.H.), (figs. 3*a*, *c*, *e*, *f*), reg. no. 1916.12.2, 3-4.

1 ♂, (damaged) collected at Schrenck, Kazakhstan. Leningrad Museum, cat. no. 1737.

1 ♀, length 15.0 mm, width 5.0 mm. Holotype of *pectinatus* Budde-Lund, collected at Schrenck, Kazakhstan. Leningrad Museum, cat. no. 1769.

2 ♂♂, length 14-15 mm, width 4.5-5.0 mm. Budde-Lund collection from Turkestan. B.M. (N.H.), reg. no. 1921.10.18, 4095-4096.

DIAGNOSIS. Body long and narrow, length 14-16.5 mm, width 4.5-5.0 mm ; colour dark grey with pale yellow tubercles. Size of tubercles varies considerably with body size, figs. 3*a*, *c*, *e*, *f* are of large male specimen with strong tuberosity ; figs. 3*b*, *d*, *g* of smaller specimen with weak tuberosity ; head with 10-12 tubercles, 6 forming a semi-circle in the middle with 2-3 in rows extending towards postero-lateral corners of head (figs. 3*c*, *d*) ; very few additional tubercles developed on head ; on large specimens head-tubercles strong, conical and pointed ; smaller specimens with weak, rounded tubercles ; lateral lobes of head large, outer edge straight or slightly convex, upper lobe somewhat pointed (fig. 3*a*) ; ratio of width of head to width of peraeon tergite 2 is about 1 : 1.6 ; peraeon tergite 1, antero-lateral projection of epimera short, pointed and with sinuous lateral margin ; tergites 1-2 on specimen with strong tuberosity with large, conical, pointed tubercles along posterior and lateral margins (fig. 3*a*) ; prominent crests developed ; tergite 3 with small bulbous tubercles, tergite 4 with small laterals only, tergites 5-7 smooth ; on small specimens with weak tuberosity tergites 1-2 with small rounded tubercles (fig. 3*b*), no crests developed, tergites 3-7 smooth ; (dental formula, 1, 4-5, 14, 4-5 ; 2, 3-4, 14, 3-4 ; 3, 2-3, 12, 2-3) ; small specimens have only 12 posterior marginal tubercles on tergites 1-3 ; telson triangular with shallow dorsal depression, lateral margins concave (3*g*, *f*) ; telson more pointed in larger specimens ; antenna 2, peduncle segment 2 with small inner lobe ; flagellum about $\frac{2}{3}$ length of peduncle segment 5, flagellum segments sub-equal (fig. 3*e*) ; exopods of pleopod 1 ♂, only weakly sinuous posterior margin, inner angle not pronounced as in *klugii* (fig. 1*c*) ; pseudotracheae well developed on exopods 1-2, small on 3, rudimentary on 4-5.

DISTRIBUTION. Central Asia ; southern Kazakhstan, shores of Aral sea, valley of Syr-darya, region of Golodnaya Steppe, shores of river Ili, Kum-basy mountains ; *crenulatus* type locality in arid hills around lake Inder.

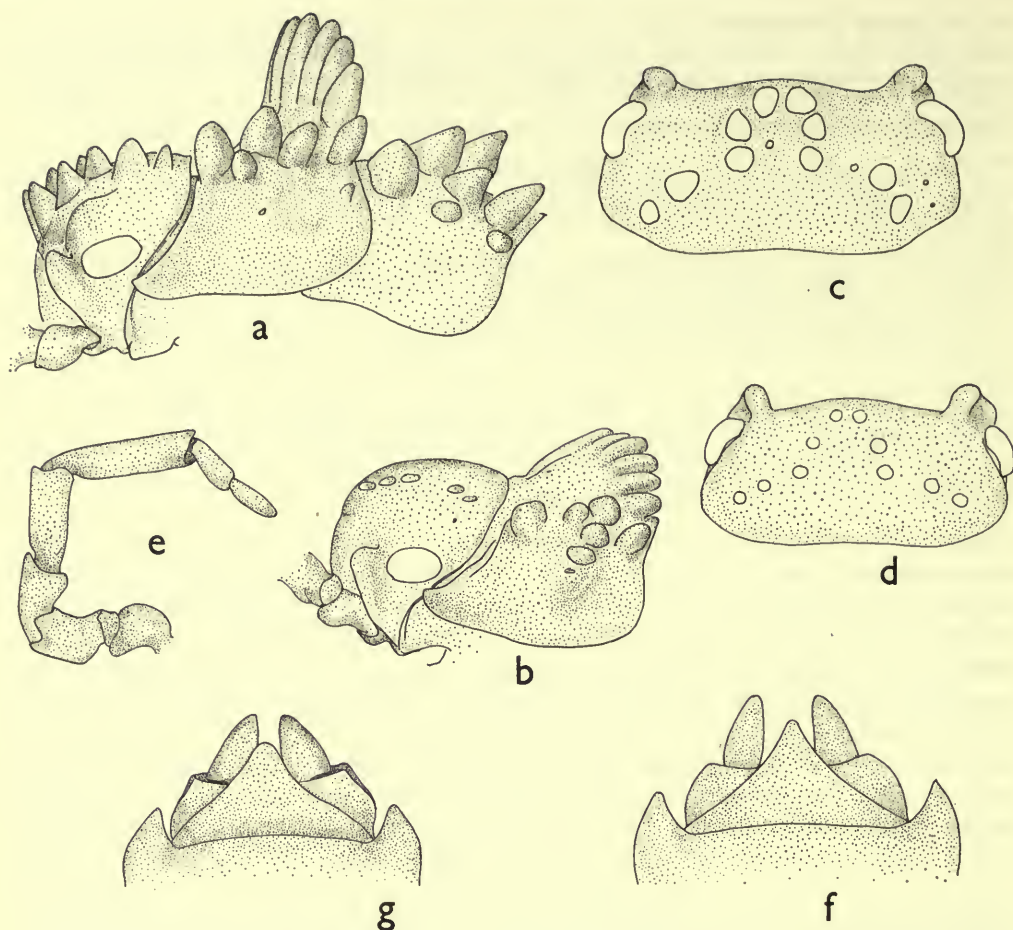


FIG. 3. *Hemilepistus crenulatus* (Pallas) ; a, lateral view of head and tergites 1-2 (large specimen) ; b, lateral view of head and tergite 1 (small specimen) ; c, dorsal view of head (large specimen) ; d, dorsal view of head (small specimen) ; e, antenna 2 ; f, telson (large specimen) ; g, telson (small specimen) ; bar scale 1 mm.

3. *Hemilepistus* (H.) *reaumuri* (Audouin & Savigny, 1826)
(text-figs. 4a-d)

Porcellio Reaumurii Audouin & Savigny, 1826 : 13 ; Milne-Edwards, 1840 : 170.

Porcellio clairvilli Brandt, 1833 : 179.

Porcellio syriaceus Koch, 1847.

Hemilepistus Reaumurii ; Budde-Lund, 1879 : 4 ; 1885 : 155.

Hemilepistus reamurii ; Dollfus, 1892 : 10 ; 1894 : 3 ; 1896 : 546 ; Richardson-Searle, 1926 : 206 ; Cloudsley-Thomson, 1955 : 248 ; Borutzky : 1958, 1471.

Paraniamba tuberculata Collinge, 1914 : 206

Hemilepistus palaestinus Verhoeff, 1931 : 38.

Hemilepistus bodenheimeri Verhoeff, 1931 : 40.

MATERIAL EXAMINED. 18 ♂♂, 11 ♀♀, length 15–22 mm, width 5.5–8.0 mm. Budde-Lund collection from various localities ; Tunisia, Cyrenaica, Algeria (Biskra and Algiers). B.M. (N.H.).

49 ♂♂, 34 ♀♀, length 17–22 mm, width 6.0–7.5 mm. Various localities and collections from southern Tunisia, Algeria (Biskra), northern Sinai, Negev desert, eastern Egypt (Manyut). B.M. (N.H.)

2 ♂♂, 1 ♀, length 14–16 mm, width 5.0–8.0 mm. Collected by Bodenheimer around Jerusalem, Palestine. B.M. (N.H.), reg. no. 1970, 195.

2 ♂♂, length 20 mm, width 7.0 mm. Syntypes of *palaestinus* Verhoeff, from Palestine. B.M. (N.H.), reg. no. 1931.4.27, 65–67.

13 ♂♂, 13 ♀♀, (17 juveniles), length 16–19 mm, width 6.0–6.5 mm. Syntypes of *palaestinus* Verhoeff ; Verhoeff collection from Jerusalem, Palestine. Munich Museum.

1 ♀, length 15 mm, width 5.5 mm. Syntype of *bodenheimeri* Verhoeff, from Palestine. B.M. (N.H.), reg. no. 1931.4.21, 68.

1 ♂, 4 ♀♀, (3 juveniles), length 10–16 mm, width 4.0–6.0 mm. Syntypes of *bodenheimeri* Verhoeff ; Verhoeff collection from Jerusalem, Palestine. Munich Museum.

1 ♂, 3 ♀♀, length 11–12 mm, width 4.0–5.0 mm. Collected by Verhoeff in Palestine. B.M. (N.H.), reg. no. 1938.7.7, 41–44.

2 ♂♂, 3 ♀♀, length 20–21 mm, width 6.5–7.0 mm. Collected by Verhoeff in Palestine. B.M. (N.H.), reg. no. 1938.7.7, 35–40.

8 ♂♂, 7 ♀♀, length 18–23 mm, width 6.5–8.0 mm. Collection from Algeria (Biskra). Copenhagen Musuem.

DIAGNOSIS. Body broad, length 11–23 mm, width 4.0–8.0 mm, slate grey in colour with lighter grey epimera and whitish tubercles ; head with a large number (25–30) of small, pointed tubercles in a characteristic pattern ; pattern consists of large circle in middle of head, a group of tubercles in postero-lateral corners, and 8–10 tubercles in transverse row along posterior margin (fig. 4b) ; lateral lobes of head prominent, upper lobe rounded, outer edge straight or convex (fig. 4a) ; ratio of width of head to width of peraeon tergite 2 is about 1 : 1.8 ; peraeon tergites 1–3 with large number of small tubercles, never developed into crest ; tubercles in middle of tergites pointed, lateral group somewhat rounded and flattened ; peraeon tergite 1 with posterior marginal row of tubercles, 4 tubercles in transverse median row, and 2 anterior marginal tubercles ; tuberosity on tergites 2–3 similar to that of tergite 1 except no anterior marginal tubercles ; tergite 4 with weak tuberosity ; sometimes faint traces of tubercles on tergites 5–7 ; (dental formula, 1, 10–15, 14–16, 10–15 ; 2, 8–12, 14–16, 8–12 ; 3, 5–8, 14–16, 5–8) ; all tubercles small and number very variable ; telson triangular at base, deep dorsal depression, margins concave, apex acutely rounded (fig. 4d) ; antenna 2, peduncle segment 2 with very large inner lobe ;

flagellum half length of peduncle segment 5 ; flagellum segment 1 markedly longer than 2 (fig. 4c) ; exopods of pleopod 1 ♂, sinuous posterior edge and prominent inner angle as in *klugii* (fig. 1c) ; pleopods pigmented ; pseudotracheae 1-2 large, 3-5 rudimentary.

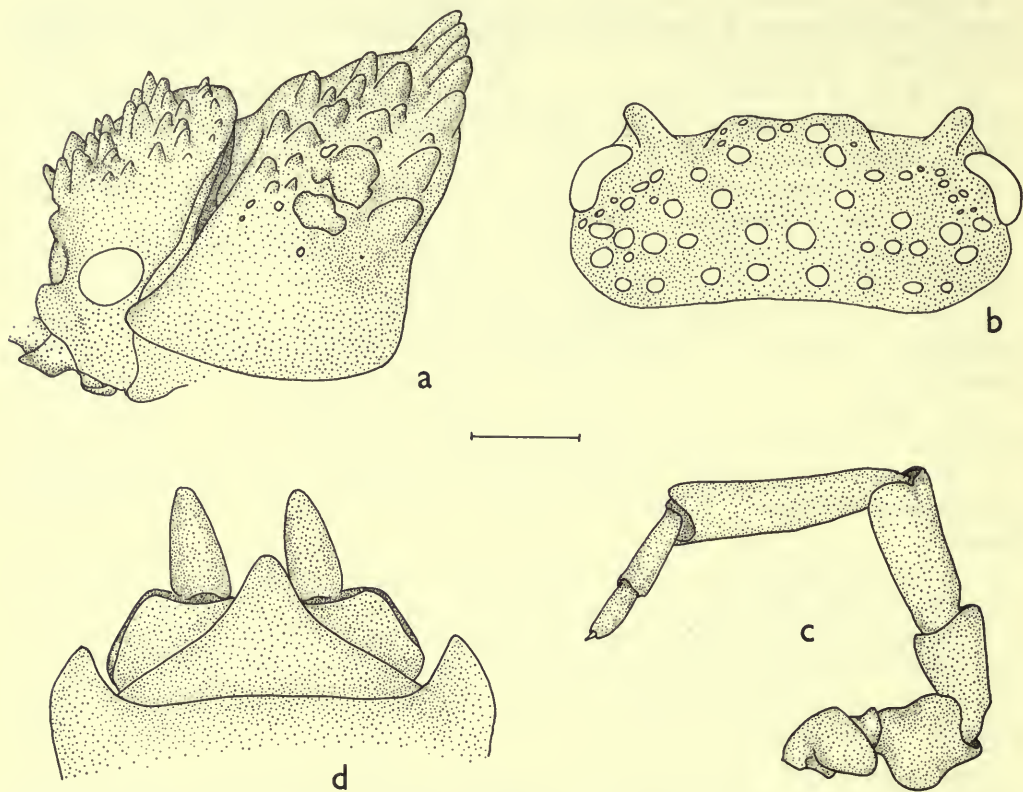


FIG. 4. *Hemilepistus reaumuri* (Audouin & Savigny) ; a, lateral view of head and tergite 1 ; b, dorsal view of head ; c, antenna 2 ; d, telson ; bar scale 1 mm.

DISTRIBUTION. Widely spread through Syria, Palestine, Egypt, Libya, Tunisia and western Algeria. According to Vandel (1955) it rarely occurs west of the meridian of Algiers.

REMARKS. Verhoeff (1931) describes two new species of *Hemilepistus* from the neighbourhood of Jerusalem—*palaestinus* and *bodenheimeri*. The diagnosis of *palaestinus* was based upon the stronger armature of tubercles on the head and anterior three peraeon tergites, and the more spinose nature of the tubercles. Syntype material from the Verhoeff Collection in Munich Museum, and from the British Museum (Natural History), was examined together with material collected in many localities in North Africa, Israel and Syria. The degree of development of the tubercles is very variable and as a result of this work *palaestinus* and *reaumuri* are

considered to be a single species. The *bodenheimeri* type specimens are small in size, a greyish brown colour, with white epimera. The tuberosity on the head and first three peraeon tergites is similar to *reaumuri* but only weakly developed. The telson is more triangular in shape than the telson of adult *reaumuri*, although it resembles the telson of small and juvenile *reaumuri*. A triangular telson is typical of the young stages of a number of species of *Hemilepistus*. The above features suggest that the *bodenheimeri* specimens are in fact small individuals of *reaumuri*. Without additional data concerning their distribution they are considered as a single species.

4. *Hemilepistus* (H.) *cristatus* Budde-Lund, 1879

(text figs. 5a-h)

Porcellio klugii ; Lessona, 1867 (not Brandt) : 187.

Hemilepistus cristatus Budde-Lund, 1879 : 4 ; 1885 : 153 ; Borutzky, 1945 : 193 ; 1958 : 1467.

Hemilepistus elegans ; Walter, 1889 : 1110.

Hemilepistus crenulatus ; Arcangeli, 1932 (part) : 1.

?*Hemilepistus uljanini* Borutzky, 1955 : 216 ; 1958 : 1469.

MATERIAL EXAMINED. 1 ♂, 1 ♀, length 17 mm, width 5.0 mm. Syntypes *cristatus* Budde-Lund, collected from " Serdscen in Persia ". B.M. (N.H.), reg. no. 1956. 10.10, 156-157.

1 ♂, 3 ♀♀, length 17-18 mm, width 4.5-5.0 mm. Norman collection from " Serdscen in Persia ". B.M. (N.H.), reg. no. 10443, 46.

2 ♂♂, 12 ♀♀, length 15-19 mm, width 4.5-6.0 mm. No locality. B.M. (N.H.), reg. no. 1970, 197.

DIAGNOSIS. Body long and narrow, length 15-17 mm, width 4.5-6.0 mm, dark grey body, tubercles pale yellow ; head with 16-20 short conical tubercles in characteristic pattern within a triangular area ; pattern consists of a large circle of 8 tubercles in middle of head, with lateral rows of 3-4 tubercles extending to postero-lateral corners (fig. 5b) ; sometimes 2-3 tubercles in centre of circle, and a number of smaller tubercles within the triangular area ; head tuberosity rather variable (figs. 5c-f), and in an extreme case the pattern is not apparent because the tubercles are poorly developed and flattened (fig. 5f) ; lateral lobes of head prominent, with rounded apex and sinuous outer edge (fig. 5a) ; ratio of width of head to width of peraeon tergite 2 is about 1 : 1.5 ; peraeon tergite 1, antero-lateral projection of epimera long, pointed and upturned at apex (fig. 5a) ; peraeon tergites 1-3 with well developed tubercles which may form tall upright crests on tergites 1-2 ; tergite 4 with weak tuberosity, best developed laterally ; tergites 5-7 smooth ; most anterior tubercle of tergite 1 largest, rectangular ; (dental formula 1, 4, 14, 4 ; 2 & 3, 3, 12, 3) ; telson triangular, shallow dorsal depression, lateral margins deeply concave, apex acutely rounded (fig. 5g) ; antenna 2, peduncle segment 2 with large inner lobe ; flagellum half length of peduncle segment 5 ; flagellum segments sub-equal or nearly so (fig. 5h) ; exopods of pleopod 1 ♂, strongly sinuous posterior margin, inner angle broad and rounded but less prominent than *klugii* (fig. 1c) ; pseudotracheae on 1-2 large, 3 small, 4-5 rudimentary.

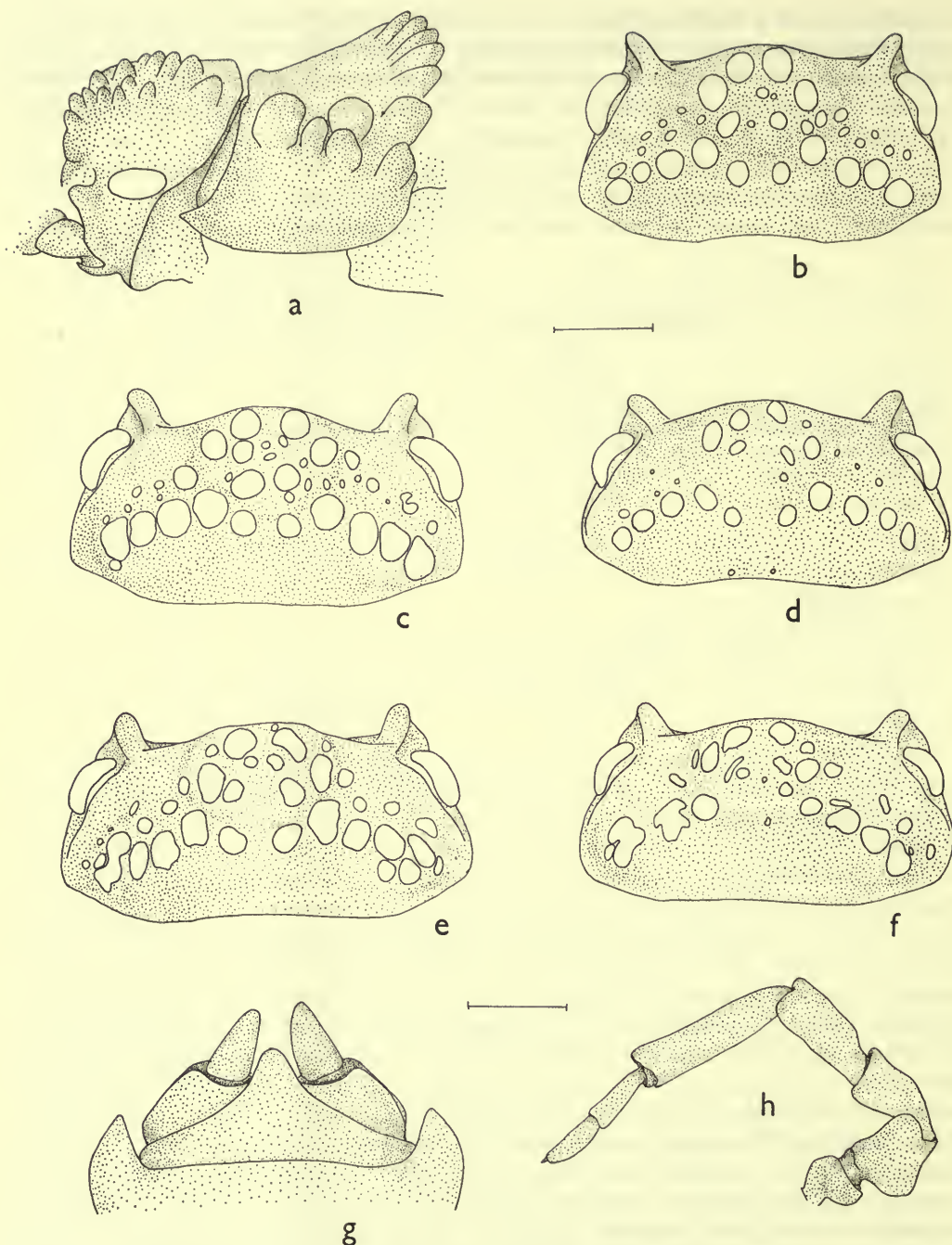


FIG. 5. *Hemilepistus cristatus* Budde-Lund ; a, lateral view of head and tergite 1 (Syntype) ; b, dorsal view of head (Syntype) ; c-f, dorsal view of head ; g, telson (Syntype) ; h, antenna ; z (Syntype) ; bar scale 1 mm.

DISTRIBUTION. Iran ; central Asia, slopes of Kopet-Daga from Serakhs to Kazandzhik, valley of Sumbar Uzboy ; Ashkhabad ; type locality Serdscen in Iran.

REMARKS. Borutzky (1955) describes a new species from Turkmeniya—*uljanini*. This seems to differ from *cristatus* only in the detailed tuberosity of the head. However, it is clear that there is considerable variation in the size and arrangement of tubercles on the head of *cristatus* and the description of *uljanini* falls within this range. In other features given *uljanini* and *cristatus* appear to belong to the same species.

5. *Hemilepistus* (H.) *magnus* Borutzky, 1945

(text-figs. 6a-d)

Hemilepistus (H.) *magnus* Borutzky, 1958 : 1467.

MATERIAL EXAMINED. 1 ♂, length 26 mm, width 10.5 mm, Budde-Lund collection from Turkmenistan. B.M. (N.H.), reg. no. 1921.10.18, 4146.

DIAGNOSIS. Largest body size for species of *Hemilepistus*, length 26–30 mm, width 9.0–10.5 mm, peraeon nearly uniform in width, tergites 5–7 a little broader than rest ; colour grey ; according to Borutzky (1958) the ventral surface is dark grey with yellow spots ; head with 12–14 long, slender tubercles in characteristic pattern (fig. 6b) ; 6 largest tubercles form an open semi-circle on front of head, with rows of 3–4 tubercles extending to postero-lateral corners ; all tubercles on head very long, slender and rounded at apex ; lateral lobes of head small ; upper part of lateral lobe rounded outer margin concave (fig. 6a) ; ratio of width of head to width of peraeon tergite 2 is about 1:2.0 ; peraeon tergite 1, antero-lateral projection of epimera short, rounded ; postero-lateral angle of epimera on tergite 1 forming an acute, backwardly pointing, process (fig. 6a) ; peraeon tergites 1–3 with very long tubercles along posterior and lateral margins ; all tubercles long, slender, cylindrical, and well spaced apart ; tergite 4 with weak tuberosity, tergites 5–7 with traces of tuberosity, best developed laterally ; epimera of tergites 6–7 markedly swollen ; (dental formula 1 & 2 & 3, 3–5, 12–13, 3–5) ; pleon short and broad ; epimera of pleon long, pointed and curved upwards a little at apex ; telson wide at base, long and with acutely rounded apex, margins sinuous (fig. 6d) ; dorsal surface of telson flat or very weakly concave ; antenna 2 strongly developed, peduncle segment 2 with small inner lobe, flagellum half length of peduncle segment 5 ; flagellum slender, segment 2 half length of 1 (fig. 6c) ; exopods of pleopod 1 ♂, sinuous posterior margin and rounded inner angle, but less pronounced than *klugii* (fig. 2c) ; pleopods pigmented.

DISTRIBUTION. Turkmeniya, Fergana valley and the region of the Alayli mountains.

6. *Hemilepistus* (H.) *reductus* Borutzky, 1945

Hemilepistus (H.) *reductus* Borutzky, 1945 : 495 ; 1958 : 1468.

MATERIAL EXAMINED. None.

DIAGNOSIS. Body small, elongate, length 13–16 mm, width 4.5–5.0 mm ; dark

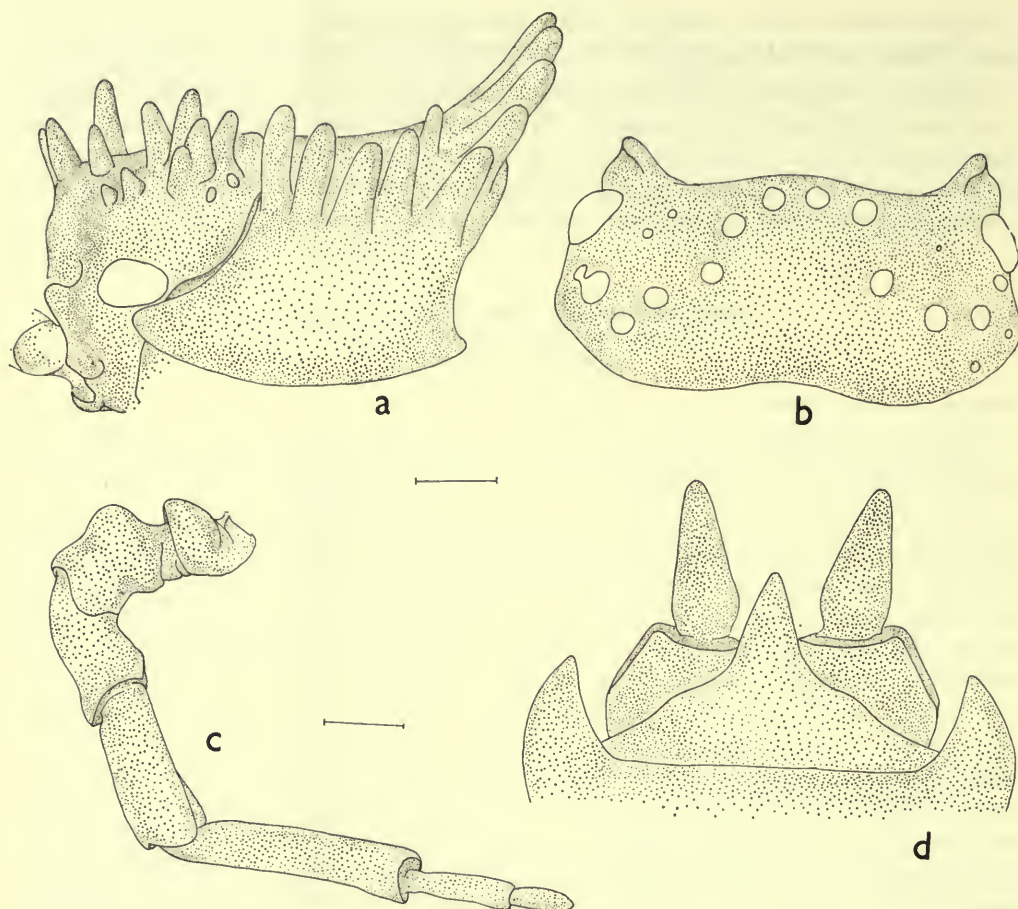


FIG. 6. *Hemilepistus magnus* Borutzky ; a, lateral view of head and tergite 1 ; b, dorsal view of head ; c, antenna 2 ; d, telson ; bar scale 1 mm.

grey with lighter epimeral margins, tubercles whitish in colour ; head with about 12 small tubercles arranged in two curved rows extending from poster-lateral corners of head to an apex at front ; additional smaller tubercles may be present on the head ; lateral lobes of head short, upper edge straight ; ratio of width of head to width of peraeon tergite 2 is about 1 : 1.5 ; tubercles present on posterior and lateral margins of peraeon tergites 1-2 ; tergite 1 with well developed laterals, but posterior row very much reduced in the middle of the tergite ; tubercles on peraeon tergite 2 larger than on tergite 1, uniform in size and closely set together ; tergite 3 with only a trace of lateral tuberosity, posterior margin smooth ; tergites 4-7 smooth ; (dental formula 1, 4-7, 12-16, 4-7 ; 2, 4-7, 10-14, 4-7) ; antenna 2, peduncle segment 5 a little longer than flagellum ; flagellum segments sub-equal ; exopods of pleopod 1 with less sinuous posterior margin than *klugii* (fig. 2c), and no lobe at inner angle.

DISTRIBUTION. Kazakhstan ; Kumak, Kara-darya, the environs of the towns of Katta-Kurgan ; widely distributed in the valley of the river Zeravshan.

7. *Hemilepistus (H.) rhinoceros* Borutzky, 1958

Hemilepistus (H.) rhinoceros Borutzky, 1958 : 1469, fig. 8.

MATERIAL EXAMINED. None.

DIAGNOSIS. Body small, elongate, length 13 mm, width 4.0–4.5 mm, body grey, tubercles white, epimeral margins light grey in colour ; head with a single large tubercle situated in a median position towards the front ; this tubercle is divided on posterior side into two smaller tubercles ; small group of 3–4 tubercles above the eyes ; lateral lobes of head small with rounded upper lobe ; ratio of width of head to width of peraeon tergite 2 is about 1 : 1.3 ; peraeon tergites 1–2 with small conical tubercles directed upwards on tergite 1 and backwards on tergite 2 ; tergites 3–7 smooth, without tuberosity ; (dental formula 1 & 2, 4–5, 12, 4–5) ; telson triangular, apex pointed and lateral margins straight ; antenna 2, peduncle segment 5 one to one and a half times length of flagellum ; flagellum segments sub-equal.

DISTRIBUTION. Kazakhstan ; type locality Dzhusandala near Lake Balkhash in an area of saline loess.

8. *Hemilepistus (H.) aphganicus* Borutzky, 1958

(text-figs. 7a–g)

Hemilepistus (H.) aphganicus Borutzky, 1958 : 1470.

Hemilepistus (H.) aphganicus kabulensis Borutzky, 1958 : 1471.

MATERIAL EXAMINED. 5 ♂♂, 3 ♀♀, length 15–21 mm, width 5.0–7.0 mm. Collected by the Afghanistan Boundary Commission in the region around Bala Murghab, Afghanistan. B.M. (N.H.), reg. no. 86–50.

2 ♂♂, 6 ♀♀, (2 juveniles), length 19–20 mm, width 6.5–7.0 mm. Collected by the Afghanistan Boundary Commission from Serakhs, Turkmeniya, U.S.S.R. B.M. (N.H.), reg. no. 93.2.19, 1–12.

DIAGNOSIS. Body broad, length 15–20 mm, width 5.0–7.0 mm, light brown in colour (in spirit) with pale yellow tubercles ; dry material grey ; peraeon rectangular, tergites 5–7 a little broader than rest ; head with 12–14 long, slender, rounded tubercles in a wide sinuous arc from postero-lateral corners towards the front (fig. 7b, c) ; 2–4 tubercles on centre of head, and row of 4–8 smaller tubercles along posterior margin ; arrangement of tubercles seen clearly in small individuals (fig. 7b) ; large specimens may have a number of additional small tubercles on the head (fig. 7c) ; lateral lobes of head with rounded apex, outer edge sinuous (fig. 7a) ; ratio of width of head to width of peraeon tergite 2 is about 1 : 1.7 ; peraeon tergite 1, antero-lateral projection of epimera long, apex rounded (fig. 7a) ; peraeon tergites 1–3 with long, slender, rounded tubercles along posterior and lateral margins ; middle tubercles in posterior row somewhat smaller than others ; in large individuals, with strongly

developed tuberosity, tergites 1-2 have a tall crest of long, well spaced tubercles, those on tergite 2 larger than those on tergite 1; in small individuals, crests not developed, all tubercles small, equal in size, and directed backwards; tergite 4 with small tubercles, tergites 5-7 smooth; (dental formula 1, 3-6, 14, 3-6; 2 & 3, 3-4, 14, 3-4); telson triangular, short (fig. 7e); telson shape varies with body size; figs. 7f and 7g are taken from 15 mm and 10 mm specimens respectively; at 10 mm stage, telson forms regular triangle, and at this stage head and peraeon tuberosity is just visible in characteristic pattern; antenna 2, peduncle segment 2, with prominent

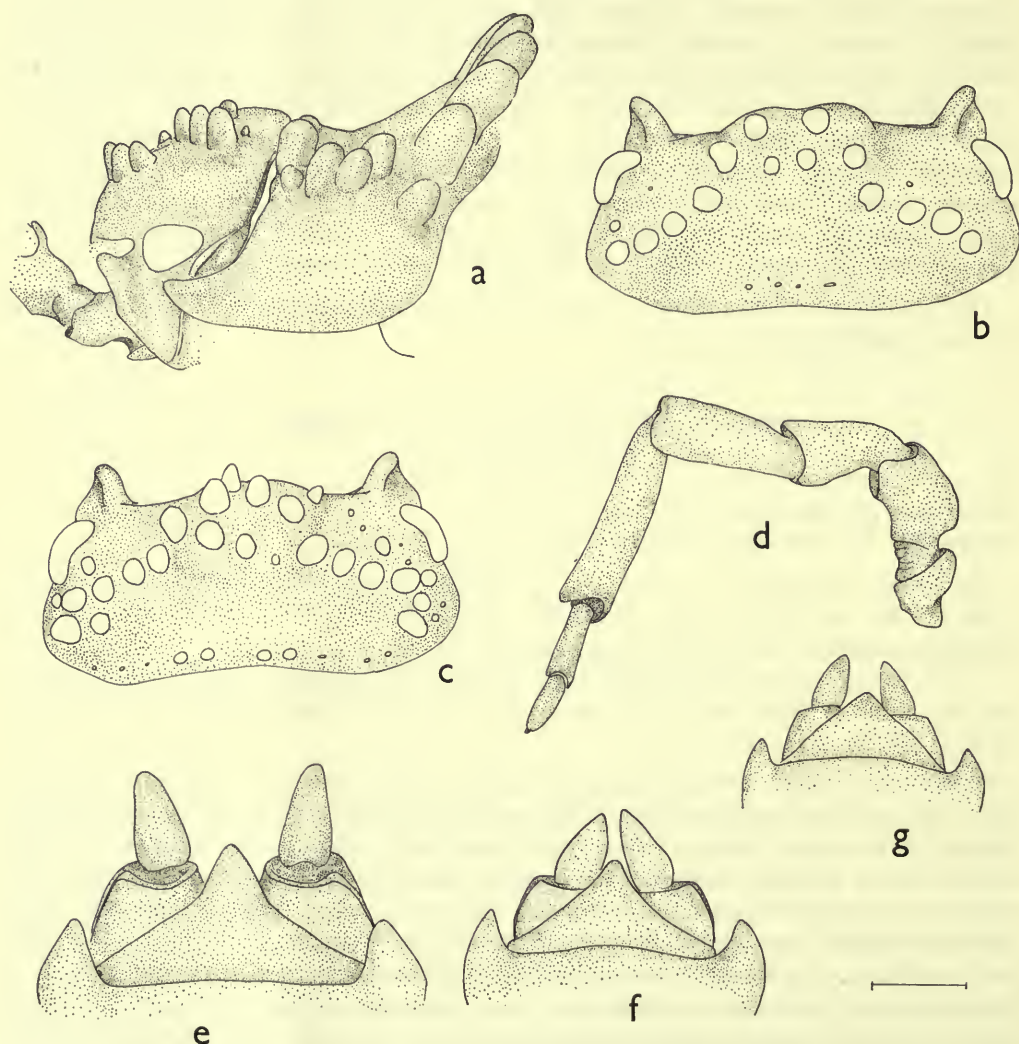


FIG. 7. *Hemilepistus aphganicus* Borutzky; a, lateral view of head and tergite 1; b-c, dorsal view of head; d, antenna 2; e, telson (20 mm body length); f, telson (15 mm body length); g, telson (10 mm body length); bar scale 1 mm.

inner lobe ; flagellum about half length of peduncle segment 5, flagellum segment 1 almost twice length of segment 2 (fig. 7d) ; exopods of pleopod 1 ♂, with markedly sinuous posterior margin and prominent inner angle as in *klugii* (fig. 1c) ; pseudotracheae on exopods 1-2 well developed, 3 small, 4-5 rudimentary.

DISTRIBUTION. Afghanistan ; Turkmeniya, U.S.S.R. ; type locality around Yakatut in Afghanistan.

REMARKS. Borutzky (1958) describes the species *aphganicus* from a small collection of dry material from Afghanistan. He also proposes a sub-species, *kabulensis* for a single female specimen from a locality near Kabul, although he adds that it may not be a valid sub-species because of the large variation between individuals of the species. The examination of the material in the British Museum (Natural History) does not justify the separation of the sub-species on the basis of the description given.

9. *Hemilepistus* (*H.*) *schirasi* n. sp.

(text-figs. 8a-f)

Hemilepistus klugii Budde-Lund, 1885 (not Brandt) : 152 (part).

MATERIAL EXAMINED. 1 ♂, 1 ♀, length 15-17 mm, width 5.5-6.0 mm. ♂ Holotype, ♀ paratype. Collected by Kollar from Shiraz in Iran. Copenhagen Museum.

1 ♂, length 16 mm, width 5.5 mm. Paratype. Collected by Kollar from Shiraz in Iran. B. M. (N.H.), reg. no. 1970 : 199.

1 ♂, length 18 mm, width 6.5 mm. Budde-Lund Collection, from Iran. B.M. (N.H.), reg. no. 1921.10.18, 4142.

DIAGNOSIS. Body broad, length 15-18 mm, width 5.5-6.5 mm, somewhat flattened dorsally ; peraeon almost rectangular, tergite 6 a little broader than rest ; all colouration lost in spirit ; head with 12-14 small, conical tubercles in sinuous line from postero-lateral corners of head towards the front (figs. 8c-e) ; no additional tubercles on head ; lateral lobes of head small, rounded, with concave outer margins (fig. 8a) ; ratio of width of head to width of peraeon tergite 2 is 1 : 1.7 ; peraeon tergite 1, antero-lateral projection of epimera short, rounded and reaching only a little beyond the posterior edge of the eye (fig. 8a) ; peraeon tergites 1-3 with small tubercles along posterior and lateral margins ; outer tubercles somewhat more bulbous than middle ones ; tergite 4 with small lateral tubercles and a trace of posterior marginal ones ; tergites 5-7 smooth, with swollen epimera ; (dental formula 1, 3-4, 14, 3-4 ; 2 & 3, 3, 14, 3) ; telson broad and short (fig. 8f) ; antenna 2, peduncle segment 2, with large inner lobe ; flagellum about half length of peduncle segment 5 ; flagellum segment 1 longer than segment 2 (fig. 8b) ; exopods of pleopod 1 ♂, with strongly sinuous posterior margin and prominent inner angle as in *klugii* ; pseudotracheae on pleopods 1-2 large, 3 small, 4-5 rudimentary.

DISTRIBUTION. The type material was collected by Kollar from Shiraz in Iran.

REMARKS. Budde-Lund (1885), in his monograph on terrestrial isopods, describes three specimens from "Schiras in Persia" as belonging to *klugii*, Brandt. These

specimens have been examined, together with the type material of *klugii* from the Berlin Museum, and it is quite clear that they are separate species. Borutzky (1958) has recognised an error in the diagnosis made by Budde-Lund and has placed "*Klugii* Budde-Lund 1885" in a list of species of doubtful validity, indicating that it may indeed be a new species.

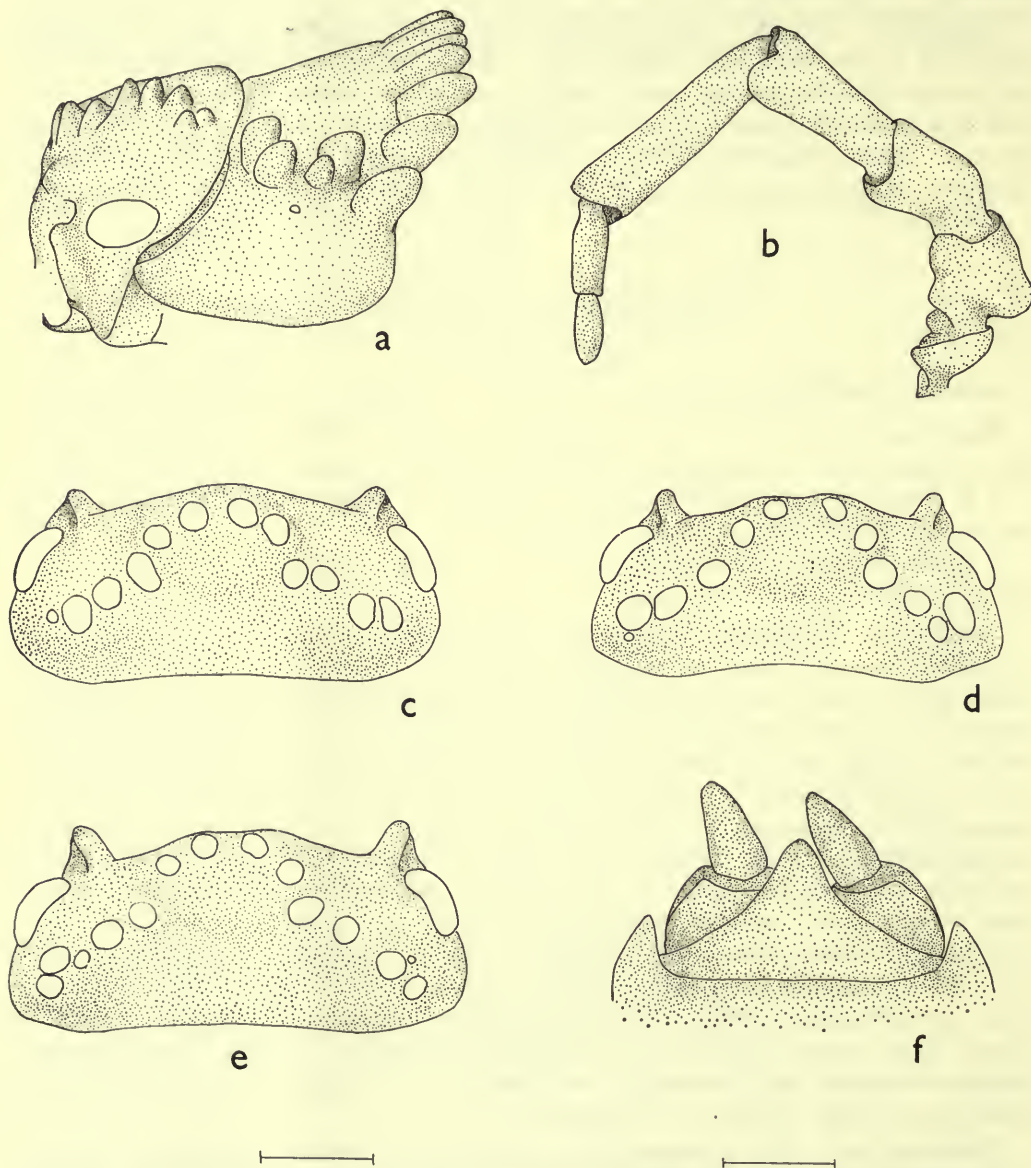


FIG. 8. *Hemilepistus schirasi* n. sp. ; a, lateral view of head and tergite 1 ; b, antenna 2 ; c-e, dorsal view of head ; f, telson ; bar scale 1 mm.

KEY TO THE SPECIES OF *Hemilepistus* (*Hemilepistus*)

- 1 Head with 10 or more tubercles on dorsal surface (2)
- Head with a single large tubercle at front, and small group of 2-4 tubercles above the eyes **rhinoceros** Borutzky
- 2 Head with 10-16 tubercles in a sinuous line from postero-lateral corners of head towards the front (3)
- Head with 16-20 large tubercles within a roughly triangular area (7)
- Head with 25-30 small tubercles, arranged as a large central ring, two postero-lateral groups and a posterior transverse row **reaumuri** (Audouin & Savigny) fig. 4
- 3 Head with 12-16 tubercles in a line from posterior corners of head towards the front ; ratio of width of head to width of peraeon tergite 2 is between 1 : 1.7 and 1 : 2.0 ; flagellum segment 1 distinctly longer than segment 2 (5)
- Head with 10-12 tubercles in a line from posterior corners of head towards the front ; ratio of width of head to width of peraeon tergite 2 is between 1 : 1.5 and 1 : 1.6 ; flagellum segments sub-equal (4)
- 4 Head, 6 large tubercles forming a semi-circle in middle and 2-3 tubercles in rows extending to postero-lateral corners ; peraeon tergite 1, posterior marginal tubercles not markedly reduced in size from sides to middle **crenulatus** (Pallas) fig. 3
- Head, 12 tubercles in two curved lines extending from postero-lateral corners to an apex at front ; peraeon tergite 1, postero-marginal tubercles markedly reduced in size from sides to middle **reductus** Borutzky
- 5 Head 12-16 long, slender, pointed tubercles ; large body size, length 18-30 mm (6)
- Head, 12 small conical tubercles in sinuous line ; small body size, length 14-18 mm **schirasi** n. sp. fig. 8
- 6 Peraeon tergites 1-3 with long, widely separate, pointed tubercles ; traces of tuberosity on tergites 4-7 ; peraeon tergite 1, postero-lateral margin of epimera with backwardly directed process ; very large body size, length 25-30 mm, width 9-10 mm **magnus** Borutzky fig. 6
- Peraeon tergites 1-4 with prominent, slender tubercles, tergites 5-7 smooth ; peraeon tergite 1, postero-lateral margin of epimera rounded ; large body size, length 18-20 mm, width 6.5-7.5 mm **aphganicus** Borutzky fig. 7
- Peraeon tergites 1-3, tubercles form either an upwardly directed crest or face obliquely backwards, ratio of width of head to width of peraeon tergite 2 is about 1 : 1.5 ; flagellum segments sub-equal ; body size, length 14-19 mm, width 4.0-5.0 mm **cristatus** Budde-Lund fig. 5
- Peraeon tergites 2-3, apices of tubercles directed backwards parallel to dorsal surface, ratio of width of head to width of peraeon tergite 2 is about 1 : 2.0 ; flagellum segment 1 longer than 2 ; body size, length 18-20 mm, width 8.5-9.0 mm **klugii** (Brandt) fig. 1 & 2

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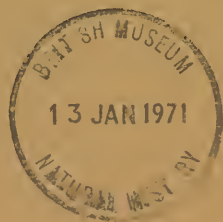


DR. R. J. LINCOLN
 Department of Zoology
 BRITISH MUSEUM (NATURAL HISTORY)
 CROMWELL ROAD
 LONDON, S.W.7

Printed in Great Britain by
Alden & Mowbray Ltd
at the Alden Press, Oxford

A TAXONOMIC REVISION OF THE
OLIGOCHAETE GENUS *EUKERRIA*

MICHAELSEN, 1935
(OCNERODRILINAE,
MEGASCOLECIDAE)



B. G. M. JAMIESON

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BY
BARRIE GILLEAN MOLYNEUX JAMIESON
University of Queensland

Pp. 131-172 ; 10 Text-figures

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By B. G. M. JAMIESON

SYNOPSIS

Material of 15 of the 27 described species of *Eukerria* has been examined and of the 21 species recognized at commencement of the study, 17 are considered valid. *E. hortensis* Stephenson, 1931; *E. peguana* Gates, 1942, *E. asilis* Righi, 1968 and *E. zonalis* (Eisen, 1893) pass into synonymy. Three infrageneric groups are recognizable from the internal structure of the calciferous glands of which two appear to be polyphyletic. The most clearly definable subgroup, a *stagnalis*-group, consisting of *E. stagnalis*, *E. papillifera* and *E. weyenberghi*, may require separate generic status when further knowledge of the morphology of these species and of the genus as a whole is acquired.

INTRODUCTION

Eukerria is a neotropical genus of the Ethiopian, Neotropical and Oriental subfamily Ocnetrodrilinae (Ocnetrodrilidae *sensu* Gates 1939, 1959). A revision of the genus has been undertaken as a contribution to a review of the Ocnetrodrilinae which is in preparation. The name *Eukerria* was proposed by Michaelsen (1935) who showed *Kerria* to be preoccupied by a protozoon. *Kerria* was erected by Beddard (1892) for *K. halophila*, a brackish water species from the upper reaches of the Pilcomayo River (Bolivia?). His description is inadequate and contains contradictions and, as no species identifiable with *halophila* has since been found, seriously hampers revision of the genus.

Prior to the present account, relatively few species of *Eukerria* had been revised since the dates of their first description. The courtesy of the authorities of the British Museum (Natural History), the Torino Museum and of the Zoologisches Museum, Hamburg, has made it possible for the author to examine material of eleven of the seventeen species of the genus recognized in the present work or fifteen of the twenty seven species which have been recognized prior to demonstration of extensive synonymy in this and other accounts. Much work remains to be done on the taxonomy and morphology of the genus, however, as examination has been limited by the poor condition of much of the long-preserved material, the short series available, and the necessity to minimize dissection of type-material.

SYSTEMATICS

Genus *EUKERRIA* Michaelsen, 1935

Prostomium variable. Setae 8 per segment in 2 closely paired couples; the interval between those of the ventral pair (*ab*) equal to that between those of the dorsal

pair (cd) ; dorsal median intersetal distance (dd) = 0.4–0.5 of the circumference (u). Nephropores presetal, from mid bc to c lines ; in a single series which is straight or nearly so on each side. Clitellum annular or saddle-shaped, in the region of XIII–XX. Prostatic pores 2 pairs, on XVII and XIX, each pore receiving the duct of a single prostate gland or very exceptionally (abnormally?) of 2 such glands. Male pores in XVIII. A seminal groove usually present on each side, connecting the male pore with the prostatic pores of the same side. Female pores paired on XIV in front of or slightly anterolateral to the ventral setal couples, (rarely in a median fissure?). Spermathecal pores 2 pairs, in 7/8 and 8/9. Dorsal pores absent.

Gizzard well developed or rudimentary in VII or absent. 1 pair of calciferous glands, in IX, with wide lumen into which project weakly or well developed septa which may fuse centrally ; or lacking septa and with thicker walls ; or (e.g. *saltensis*) intermediate in structure, having thick walls with few irregular low projections but no definite septa. Intestine commencing in XII or XIII ; typhlosome (always?) absent. Hearts in IX (always?), X and XI ; precardiac commissurals absent or forming an extensive series. Nephridia beginning in IV–XI ; avesculate or with small bladderlike ectal dilatations. Proandric ; testes and funnels in X ; free or (*stagnalis*, and *kukenthali*) in a circumcardiac testis-sac. Seminal vesicles in IX (or X?) and XI, or IX only or XI only. Prostate glands with or without muscular terminal bursae ; vasa deferentia rarely thickened ectally. Ovaries in XIII ; ovisacs absent or rarely (intraspecific variation?) present. Spermathecae with more or less distinct ducts ; adiverticulate (or, in *mcdonaldii*, with pseudo-diverticula which do not store sperm).

DISTRIBUTION. South America : Brazil ; Paraguay ; Bolivia (?) ; Argentina ; Chile. Baja California. Two species have ranges outside America : *E. kukenthali* in the West Indies, Malaya, Christmas Island (near Java) and Burma ; *E. saltensis* in South Africa, Burma, New Caledonia and Australia. The genus is usually regarded as limnic (Stephenson, 1930) but few species are known certainly to occur in aquatic habitats.

TYPE-SPECIES. *Kerria halophila* Beddard, 1892.

KEY TO SPECIES OF THE GENUS *EUKERRIA*

- | | | |
|---|---|-------------------------------------|
| 1 | Prostatic porophores, (raised approximately circular areas around the prostatic pores) extending into or meeting in XVIII | 2 |
| – | Prostatic porophores not extending into XVIII | 6 |
| 2 | Spermathecal pores in b lines | <i>E. tucumana</i> , p. 162 |
| – | Spermathecal pores a little below c lines to above d lines | 3 |
| 3 | Spermathecal pores above d lines | <i>E. eiseniana</i> s. lat., p. 136 |
| – | Spermathecal pores in or slightly below c lines | 4 |
| 4 | Prostatic porophores in contact in segment XVIII | <i>E. garmani</i> , p. 140 |
| – | Prostatic porophores (or papillae) separated in XVIII by a region equal in width to a porophore | <i>E. pascuorum</i> , p. 149 |
| 5 | Spermathecal ducts significantly shorter than the ampulla. | 6 |
| – | Spermathecal ducts hardly appreciably shorter to longer than the ampullae | 12 |
| 6 | Spermathecal pores above b lines | 7 |
| – | Spermathecal pores in or below b lines | 10 |

- 7 Gizzard small or well developed 8
 - Gizzard totally absent *E. stagnalis*, p. 153
- 8 Spermathecal duct ectally very strongly muscular and thicker than the remainder of the spermatheca. (Calciferous glands with slit-like lumen and thick, honeycombed walls) *E. limosa*, p. 146
 - Spermathecal duct not more strongly muscular ectally than elsewhere. (Calciferous glands with fairly wide lumen, into which folds of the walls project) 9
- 9 Seminal grooves in the same longitudinal line as the prostatic pores though slightly convex medianly *E. rosae*, p. 149
 - Seminal grooves distinctly median to the prostatic pores, strongly convex medianly *E. subandina*, p. 158
- 10 Gizzard well developed. Median papillae absent 11
 - Gizzard absent. Median papillae present, in XIV-XVI *E. papillifera*, p. 148
- 11 Seminal grooves present. Clitellum in XIII-XX *E. asuncionis*, p. 135
 - Seminal grooves absent. Clitellum in XIV-XIX *E. halophila*, p. 144
- 12 Seminal grooves absent 13
 - Seminal grooves present 14
- 13 Spermathecal pores in *b* lines *E. weyenberghi*, p. 163
 - Spermathecal pores near *c* lines *E. rubra*, p. 151
- 14 Seminal grooves further lateral at the male pores (in XVIII) than at the prostatic pores *E. urna*, p. 162
 - Seminal grooves straight or further median at the male pores than at the prostatic pores 15
- 15 Spermathecal pores in *ab* lines. (A median genital marking usually present in XXI) *E. kukenthali*, p. 144
 - Spermathecal pores well dorsal of *b* lines 16
- 16 Spermathecal pores in *bc* *E. saltensis*, p. 152
 - Spermathecal pores in *cd* *E. mcdonaldii*, p. 147

Eukerria asuncionis (Rosa, 1895)

Kerria asuncionis Rosa, 1895a : 2 ; Rosa, 1895b : 145 ; Michaelsen, 1900 : 370.

l = 25-45 mm, w = 2 mm, s = ca. 100. Epilobous. $aa = bc : dd : u = 0.5$. Clitellum annular, XIII-XX, weaker ventrally. Prostatic pores eye-shaped at the protuberant rounded angles of a quadratic male field which is laterally delimited by straight seminal grooves connecting the prostatic pores of each side. Female pores possibly represented by a median transverse fissure with slightly tumid lips. Spermathecal pores in front of the ventral setae.

Last septal glands in VIII. Gizzard well developed. Oesophageal diverticula large. Testes? Prostates minute, about 1 mm long, almost straight. Spermathecae pyriform, passing gradually into a short duct.

DISTRIBUTION. Paraguay.

MATERIAL EXAMINED. 4 postclitellar portions ; Torino Museum ol. 105, ex. 296, L. Borelli, 1893.

The above description is taken from Rosa (1895b).

The re-examined specimens are presumably types but, as they lack the clitellar ends,

are not certainly identifiable and yield no information. The species is inadequately defined from *E. halophila*.

***Eukerria eiseniana* (Rosa, 1895)**

Fig. 1, 2A-F, 10A

Kerria eiseniana Rosa, 1895a : 2 ; Rosa, 1895b : 141, Pl. fig. 16 ; Michaelsen, 1900 : 372.

Kerria hortensis Stephenson, 1931 : 314, Fig. 2, Pl. 17, fig. 8, Pl. 18, fig. 9.

l = 35-50 mm, w = 1.4-1.8 mm, s = 86-123 (25-55 mm, 2 mm, 90-125 (Rosa)). Epilobous $\frac{1}{2}$, margins slightly or strongly convergent, open or (1 specimen) with an indistinct posterior margin. Setae : in segment XII *aa* : *ab* : *bc* : *cd* : *dd* = 4 : 1 : 5.3 : 1.4 : 11.3 ; *dd* : *u* = 0.37 (1 specimen) but *cd* not always significantly larger than *ab* ; setae *a* present and *b* absent in XVII to XIX. Clitellum annular, weaker in *aa* to the extent, in one specimen, of appearing saddle-shaped ; XIII, $\frac{1}{2}$ XIII - $\frac{1}{2}$ XX, XX (= $7\frac{1}{2}$ -8 segments) ; intersegmental furrows weak or in XVII-XIX, totally obscured ; setae visible. Prostate pores at mid *bc* (relative to adjacent segments) on small round papillae each of which lies on a transversely oval tumescence (porophore) which fills XVII or XIX longitudinally and *b* to *c* transversely ; a straight or medianly very slightly convex seminal groove connecting the papillae of a side ; the prostatic porophores joined longitudinally by a low tumid area of approximately equal width, a male pore lying in each seminal groove where the latter intersects a transverse cleft which bisects the male field in XVIII. A pair of more or less distinctly visible presetal tumid pads (accessory genital markings) in *ab* of XX with lateral extensions to *c* lines.

Female pores inconspicuous, near the anterior margin of XIV in *b* lines. Spermathecal pores minute sometimes considerable orifices without or, in one specimen, with slightly raised rims, in $\frac{7}{8}$ and $\frac{8}{9}$ in or slightly above *d* lines.

Last septal glands anterior in VII. Gizzard glossy and globular approximately $1\frac{1}{2}$ times the width of the preceding oesophagus ; easily compressible, its wall little thicker than that of the oesophagus. Calciferous glands, each with a long somewhat twisted duct which is about as long as the large subspherical sac ; the walls thin and with numerous (approximately 30) thin radial septa of varying lengths, some reaching the centre of the lumen but none uniting across it or with adjacent septa ; lumen ciliated. Intestine beginning in XII. Hearts in X and XI ; thin commissurals in IX. Nephridia not seen anterior to IX ; ducts entering the parietes in *bc* nearer *c* than *b*. Fairly small tongue-like testes and very large iridescent much-convoluted sperm funnels free in X. Seminal vesicles very large, slightly incised, almost smooth-surfaced in IX and XI, the posterior pair the larger.

Prostates with long very muscular, ectally widening ducts which are maximally 114 μ wide ; the glandular portions tortuous but not much intertwined extending to XXXII, maximally 160 μ wide. Ovaries small with few, large oocytes and small funnels, in XIII. Spermathecae discharging anteriorly in VIII and IX each with a sac-like ampulla and spiral or somewhat twisted duct which when extended is as long as or longer than the ampulla ; the terminal region of the duct forming a slight muscular bulbus ; length of right spermathecae, moderately extended 0.82-0.88 mm.

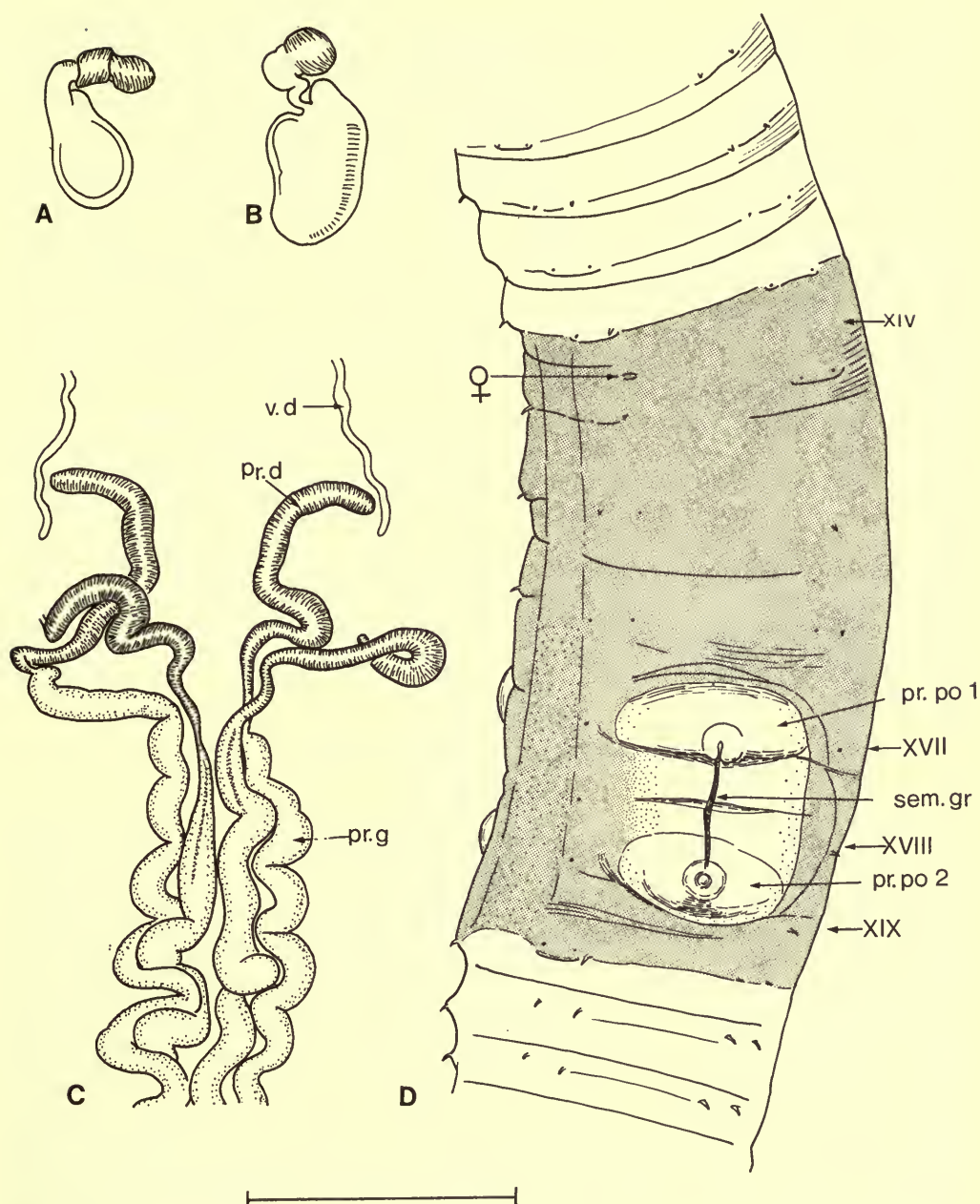


FIG. 1. *Eukerria eiseniana*. Syntype, Torino Museum, ol. 110, ex. 295. A and B, right and left spermathecae respectively of VIII; C, prostates; D, clitellar region.

DISTRIBUTION. Paraguay : Asuncion and Rio Apa (Type localities) and (*hortensis*) Makthlawaiya.

MATERIAL EXAMINED. 5 clitellate syntypes of *Kerria eiseniana*, of which 1 was dissected, Rio Apa, Paraguay, collector Borelli, 1893 ; Torino Museum ol. 110 ex. 295. A clitellate "cotype" of *Kerria hortensis*, Makthlawaiya. B.M. (N.H.) 1930. 7.30 56/66 (the latter specimen is described in the Remarks below).

REMARKS. Rosa observed in *eiseniana* ornamentation of the setae in the form of minute depressions on the tip. The clitellum was considered to be saddle-shaped. The present investigation does not confirm the contiguity of anterior and posterior prostatic porophores which he described. The contorted portion of the spermathecal ampulla described in the type description is here regarded as the ental region of the duct, the terminal bulbous of the present account being the equivalent of the duct described by Rosa. The calciferous glands were said by Rosa to be permeated longitudinally by many parallel blood vessels and the internal lumen to be large ; folding of the lining was not observed.

Kerria hortensis Stephenson, 1931, is here regarded as a junior synonym of *K. eiseniana* Rosa. Stephenson's observations have been considerably augmented in the present study and it will be of value to present a separate description of "*hortensis*" both to assemble the characteristics of this entity and to permit separate description (above) of the syntypes of *eiseniana*. The two taxa are sympatric and are the only members of the genus in which the spermathecal pores lie above the dorsalmost setal lines (*d*). Agreement in other respects is correspondingly close as the following description shows. It should be noted that Stephenson's illustrations for *hortensis* (Pl. 17, fig. 8 ; Pl. 18, fig. 9) were incorrectly labelled as pertaining to *E. limosa*.

E. hortensis (Stephenson, 1931)

Fig. 2A-F

l = 35-48 mm, w = 1-1.5 mm, s = 86-91. Slightly epilobous. In the midbody *aa* ca. = *bc*, behind the midbody slightly greater than *bc*, in front of the clitellum 1.3 *bc* ; *dd* : *u* = 0.5 in front of the clitellum, less than 0.5 behind the midbody. Nephropores not visible externally ; nephridial ducts entering the parietes immediately below *c* lines. Clitellum saddle-shaped, XIII-XX (= 8), but thickest in XII-XVI. Prostatic pores post- and pre-setal, respectively, in XVII and XIX, nearer *c* lines than *b* lines, those of a side on a large prominent oblong-oval or slightly dumb-bell-shaped area, which is sufficiently lateral (extending to *d* lines) and sufficiently prominent to be visible, standing out on each side, when the worm is viewed dorsally. Each of these male areas crossed by a transverse groove at mid-XVIII and by a longitudinal seminal groove which connects the anterior with the posterior prostatic pore. Male pores apparently at the junction of the two grooves. Female pores in *b* lines approximately midway between the setal arc and the anterior margin of XIV, round orifices without appreciable lips. Spermathecal pores in 7/8 and 8/9 approximately midway between setae *d* and the dorsal midline, each bounded anteriorly and posteriorly by a strongly protuberant lip.

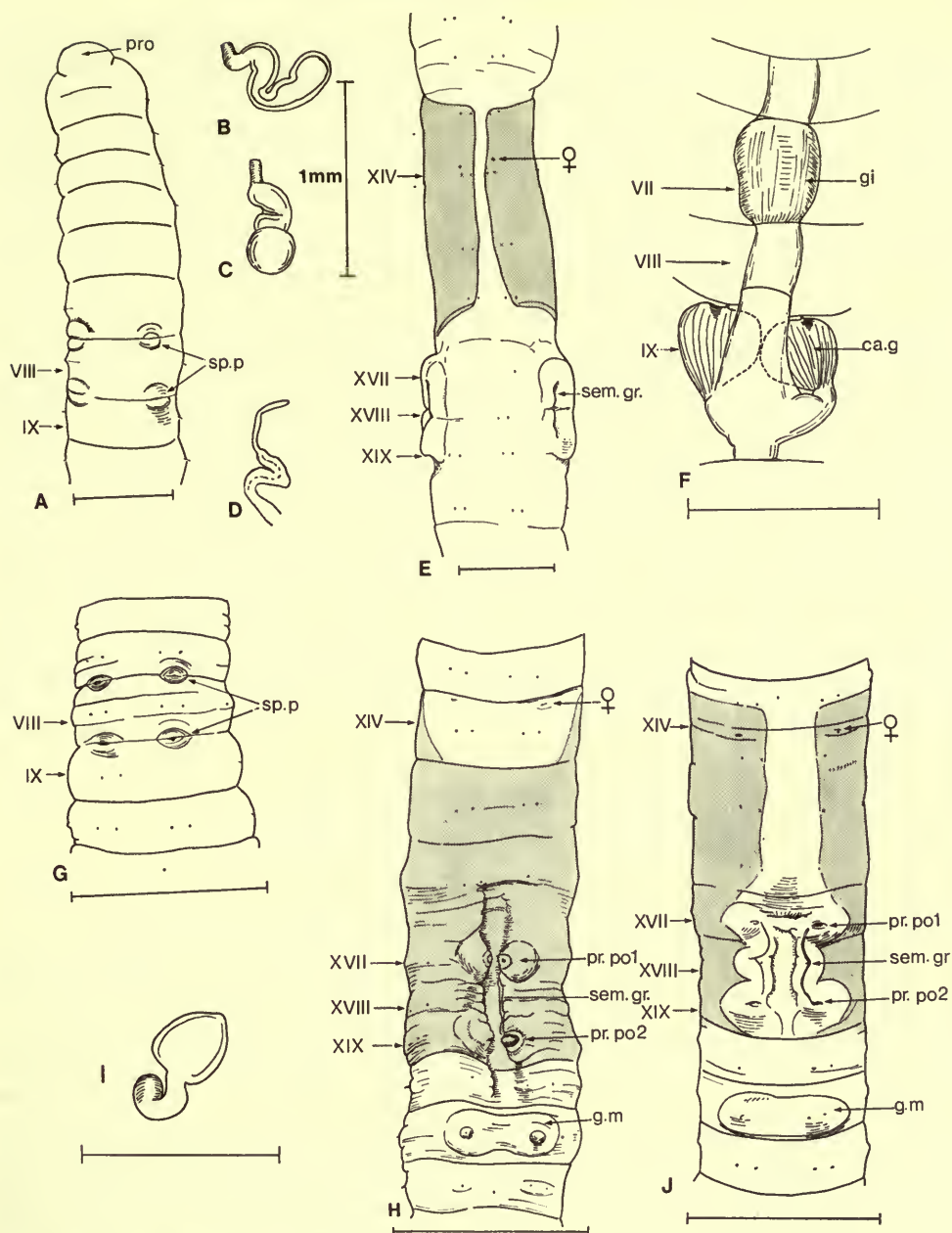


FIG. 2. A-F. *Eukerria eiseniana*. ("cotype" of *E. hortensis*, B.M. (N.H.) 1930.7.30. 56) : A, dorsal aspect showing spermathecal pores ; B and C spermathecae ; D, anterior end of a prostate gland ; E, clitellar region ; F, calciferous glands and gizzard. G-J, *E. kukenthali*, G, Christmas Island specimen, B.M. (N.H.) 1934.3.12.40, dorsal aspect showing spermathecal pores ; H, clitellar region of same ; I, left spermatheca of IX of type-specimen, Hamburg Museum, V. 7188 ; J, clitellar region of cototype of *E. selangorensis*, B.M. (N.H.), 1933.2.14.62.

Gizzard almost twice the width of the oesophagus but easily compressible and not strongly muscular. Calciferous glands stoutly pear-shaped, almost subspherical, with the wide end anterior ; each considerably wider than the oesophagus, from which it arises by a short thick stalk dorsolaterally, and adpressed to that of the other side below the oesophagus; thin walled, with 20–25 narrow longitudinal ridges projecting well into the lumen but not in contact centrally. Intestine beginning anteriorly in XII, with distinct oesophageal valve. Dorsal vessel continued onto the pharynx. Hearts in X and XI large and latero-oesophageal ; in IX smaller and dorso-ventral only. Nephridia with preseptal funnels ; commencing in VI ; present in the spermathecal and gonadial segments. Testes large and tongue-like, funnels much convoluted, free in X. Each vas deferens throughout the length of XI forming a wide, gently curved seminal reservoir tapering from the funnel ; seminal vesicles small, in XI only (in IX also in a sectioned specimen, Stephenson). Glandular portions of the prostates much intertwined and irregularly winding, extending posteriorly through several segments ; ducts abruptly demarcated, about one-fourth the width of the glandular portions and about the length of a segment, lacking a muscular sheen. Ovaries well developed, with several united egg strings, in XIII. Ovisacs apparently absent. Spermathecae tubular, the ental portion being somewhat but not much wider than the rest, there being no sharp distinction between one part and the other. A short terminal portion, which may be called the duct, is however, narrow and muscular. Length of two spermathecae, *in situ*, 0.6 mm of which about one fifth comprises the muscular duct. The spermatheca is strongly bent on itself at about the middle of its length.

Eukerria garmani (Rosa, 1895)

Eukerria garmani garmani (Rosa, 1895)

Fig. 3 A–E, 10B

Kerria garmani Rosa, 1895a : 2 ; 1895b : 139, Pl. fig. 14, 15 ; Michaelsen, 1900 : 371.

l = 56 mm, w = 1.3 mm, s = 124. (50–55 mm, 1 mm, 150 segments (Rosa, 1895b)). Proepilobous (1 specimen) to broadly epilobous, closed 1/3 (2 specimens). In XII, $aa : ab : bc : cd : dd = 5 : 1 : 5 : 1 : 13$; $dd : u = 0.41$ ($aa < bc$) (Rosa) ; Setae *b* absent in XVII–XIX ; setae *a* present or sporadically absent Nephropores? Clitellar limits indeterminable. (Saddle-shaped on $\frac{1}{2}$ XIII– $\frac{1}{2}$ XX interrupted between the ventral setae and by the male genital field (Rosa)). Prostatic pores minute, at approximately $\frac{1}{4}$ *bc* above *b* lines, and equatorial, in XVII and XIX, each on a large porophore, widest longitudinally which fills its segment longitudinally and impinges onto XVIII so that only a small “waist” intervenes between the two porophores of a side ; each porophore inflated or depressed and auricular ; the lateral borders of the porophores, reaching approximately to $\frac{1}{2}$ *bc*, well defined, the median borders, in *b* lines, indistinct. Male pores minute, at the sites of the absent setae *b* of XVIII, the narrow distinct seminal grooves running almost straight and medianwards to them from the prostatic pores of the corresponding side ; each groove bounded laterally, between the porophores, by a wide low, tumid border. The entire ventral

surface in XVII–XIX, between the prostatic porophores may be elevated as a cushion-like area of which the porophores form the rounded corners. Intersegmental furrows 17/18 and 18/19 obscured ; those on the remainder of the clitellum visible. Female pores inconspicuous, near the anterior border of XIV, immediately lateral of (or in (Rosa)) *b* lines. Spermathecal pores elliptical white areas, approximately the width of a setal couple, with their median limits at mid *bc* (centres a little median of the dorsal setae (Rosa)). Accessory genital markings : an indistinct midventral tumescence in XIII, filling the presetal region longitudinally and laterally extending to *a* lines (3 specimens).

Last septal glands in VII. Gizzard almost unrecognizable, the oesophagus elongated in VII but its walls transparent and only a little thicker than those of the oesophagus in VIII (the musculature comprising $\frac{3}{4}$ of the total thickness of the walls (Rosa)). Calciferous glands arising ventrolaterally from the oesophagus. (In the single specimen examined that on the right is a rudimentary, broadly digitiform diverticulum lying parallel to and lateral to the oesophagus and reaching anteriorly only to $\frac{1}{2}$ IX from septum 9/10 whereas that on the left fills the segment longitudinally lying beneath and projecting laterally beyond the oesophagus). Intestine originating anteriorly, and with abrupt expansion, in XII ; typhlosome absent. Hearts in X and XI ; slender commissurals in IX ; supra-oesophageal vessel seen in XI. Testes narrow, tongue-like ; sperm funnels iridescent ; free. Seminal vesicles in IX and XI very large, each deeply dissected into several distinct lobes which are themselves lobulated ; approximately equisized in the two segments. Prostates ending in XXXVII (passing at least to XXVIII (Rosa)), coiling in the first few segments and then running almost straight ; their ducts ca. 1 mm long reaching a maximum width, near their ectal ends, of 115 μ , demarcated from the glands by their muscular sheen, the ducts and glands narrower at their junction. Ovaries broadly paddle-shaped ; funnels small ; ovisacs absent. Spermathecae each more or less contorted, with an irregular saclike ampulla constricted off from a shorter duct which consists of an ectal muscular portion and an ental inflated portion which might be considered part of the ampulla ; total length (a right spermatheca of VIII) 0.97 mm.

DISTRIBUTION. Central Paraguay.

MATERIAL EXAMINED. Several syntypes of which three have the male fields developed, all badly softened, Central Paraguay, collector Borelli, 1893 ; Torino Museum, ol. III, Ex. 293.

REMARKS. Rosa (1895b) observed ornamentation of the setae in the form of semilunar depressions near the tip, larger but less numerous than those in *E. papillifera*. His description of the male genital field applies well to the specimen here illustrated in fig. 3A though anterior and posterior porophores are not contiguous in the latter, but does not cover all variations. The statement that the intestine commences in XIII is not confirmed. His interpretation of the form of the spermathecae agrees in essentials with the author's though he did not recognize the existence of a distinct duct. It was as follows: the spermatheca is large, sessile, without diverticula and each forms a large tube contorted into a spiral, a slight constriction permits recognition of two chambers of which the first, which is the shorter, has a columnar

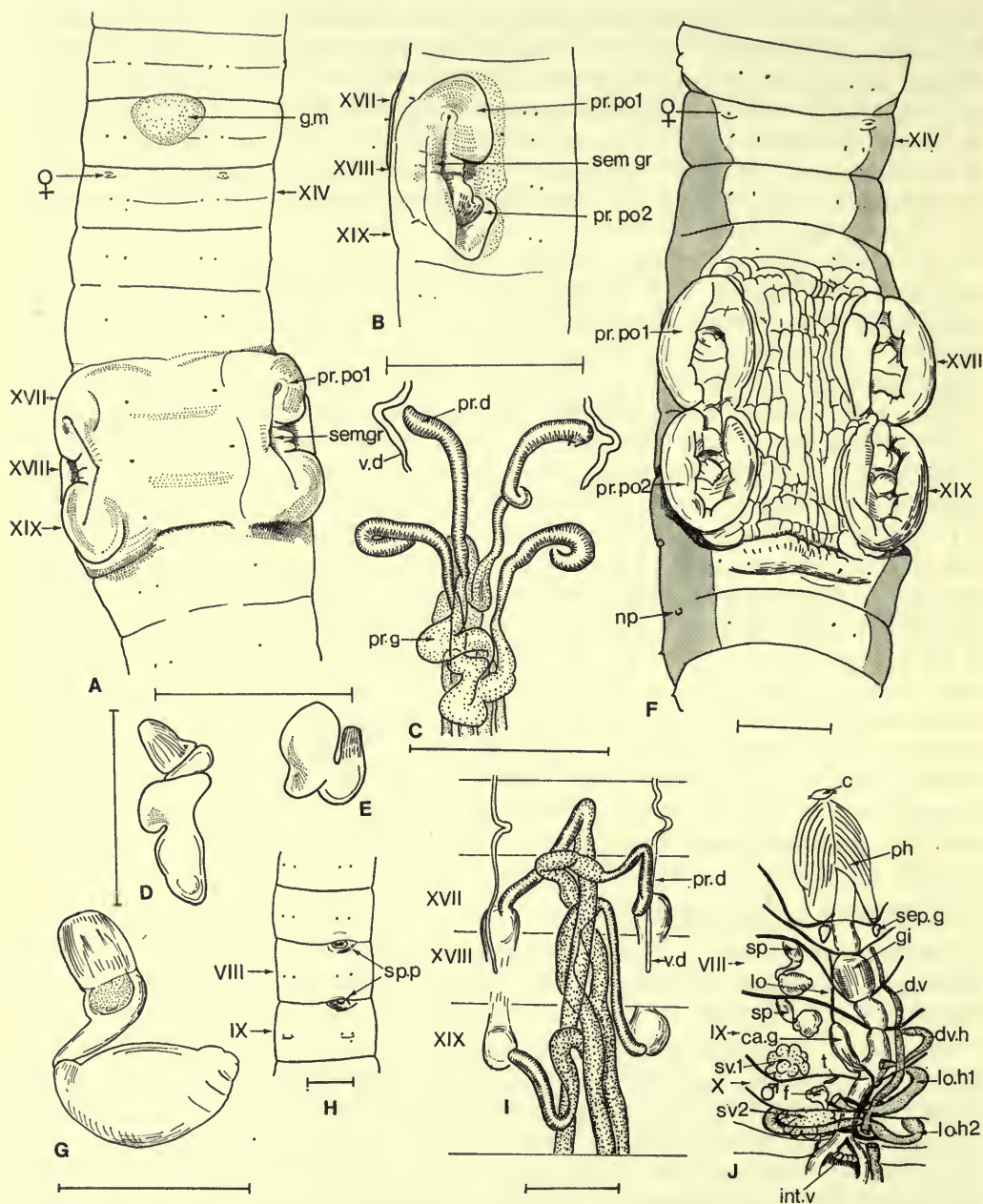


FIG. 3. *Eukerria garmani*. A-E, syntypes, Torino Museum, ol. 111, ex. 293 : A and B, genital regions of two syntypes ; C, prostates ; D and E, right spermathecae of VIII and IX respectively, of latter specimen. F-J, *E. garmani argentinæ* subsp. nov., holotype, B.M. (N.H.) 1949.3.1.1165 : F, clitellar region ; G, spermatheca ; H, spermathecal pores ; I, prostates ; J, anterior dissection.

epithelium higher and more regular than that of the second chamber of which the walls are more glandular. The first chamber tapers gradually without differentiation of a duct, to the external aperture; the part nearest the body wall being invested in a strong muscular sheath.

Poor preservation has prevented description of the nephridia.

Eukerria garmani argentinae subsp. nov.

Fig. 3 F-J

1 = 62-136 mm (14 clitellate specimens). Indistinctly epilobous, open, $\frac{1}{2}$. In XII, $aa : ab : bc : cd : dd = 3 : 1 : 3.5 : 1 : 9.25$, $dd : u = 0.40$ (1 specimen); ventral setal couples obscured (absent?) in XVII-XIX. Nephropores not generally visible but evident on the clitellum as white circular prominences, anterior in their segments and a little above mid bc . Clitellum saddle-shaped, $\frac{1}{2}$ XII-XXI, best-developed in XIV-XX, ventral margins shortly above b lines. Prostatic pores shortly lateral of b lines at the depressed puckered centres of very large inflated, longitudinally oval porophores, those of XVII contiguous with those of XIX, the rims of the porophores interrupted or lower at the region of contact. No definite seminal grooves present but the internal, median margin of the rims probably functioning as such. Male pores (from internal examination) in XVIII, intermediate between and in the same line as the prostatic pores. The area between the porophores tumid, pleated and reticulated from shortly behind the setal zone of XVI to shortly in front of the setal zone of XX; intersegmental furrows 16/17-19/20 obscured; those on the remainder of the clitellum visible. Female pores inconspicuous transverse slits with slight, parallel lips, near the anterior border of XIV, immediately lateral of b lines. Spermathecal pores fairly conspicuous elliptical clefts in c lines. Accessory genital markings (14 specimens) absent.

Last septal glands in VI. Gizzard in VII, about twice the width of the preceding oesophagus. Calciferous glands fusiform. Intestine commencing anteriorly in XII. Dorsal vessel traceable to anterior VII only; hearts of IX dorsoventral, of X and XI latero-oesophageal; no preceding commissurals recognizable; supra-oesophageal vessel arising by a vessel from each calciferous gland and ending by bifurcation to the hearts of XI; latero-oesophageal (extra-oesophageal) vessels a pair running median to the hearts, traced from anterior VII to the anterior poles of the calciferous glands; subneural vessel absent. First detectable nephridia rudimentary in XI; well developed in XII posteriorly, with large preseptal funnels; ducts slender, avesculate. Testes, funnels and sperm masses free in X, the vas deferens swollen in XI behind each funnel; seminal vesicles racemose in IX and XI. Prostates similar to those of the nominate subspecies but small indistinct bursae visible internally corresponding with the prostatic porophores. Ovaries very large and much branched, in XIII; ovisacs absent. Spermathecae with ovoid to subspherical ampulla and narrow duct of approximately the same length, a short terminal portion of which is widened and has a muscular sheen; the duct twisted axially through half to a whole turn.

DISTRIBUTION. Argentina.

MATERIAL EXAMINED. Syntypes : 14 clitellate specimens of which 2 were dissected, Loreto, Argentina, collector L. Černosvitov, 27.x. 1931, B.M. (N.H.), 1949.3.1. 1165–1194, labelled by Černosvitov “*Kerria (eiseniana var.?)*”.

REMARKS. The constant absence of the median accessory genital marking in Argentinian specimens is here tentatively considered to merit subspecific distinction from Paraguayan specimens. Černosvitov's queried identification of the Argentinian specimens as *eiseniana* is contraindicated by the location of the spermathecal pores which are dorsal to *d* lines in *eiseniana*. It, nevertheless, reflects the similarity between the latter species and *garmani*.

***Eukerria halophila* (Beddard, 1892)**

Fig. 9A

Kerria halophila Beddard, 1892 : 355, Fig. 1, 2 ; Beddard, 1895 : 556 ; Michaelsen, 1900 : 370.

l = 25–38 mm, w = 1 mm, s ? Setae closely paired and unmodified throughout ; persistent on the genital segments. Clitellum annular, XIV–XIX. Prostatic pores on the summit of elevations ; the anterior pores a little anterolateral to setae *b* of XVII ; the posterior pores slightly behind the ventral setae of XIX ; male pores in the setal zone and lateral to *b* of XVIII. (This textual distribution differs from Beddard's illustration in which anterior prostatic pores are postsetal and very slightly lateral to *b* lines of XVII and posterior prostatic pores are presetal in *a* lines of XIX ; and the male pores are lateral to setae *b* of XVIII). Female pores on XIV. Spermathecal pores 2 pairs, in 7/8 and 8/9, in *ab* lines.

Gizzard well developed, in VII. Oesophageal diverticula with much folded internal walls, in IX. Intestine commencing in XIII. Nephridia present in the genital segments. Prostates fairly wide ; extending through several segments bent or recurved once ; with narrow muscular duct about one fourth the length of the glandular part ; the latter with a single layer of cells. Testes and very large sperm funnels free in X. Sperm sacs in X and XI, “partially involve” the testes and sperm funnels. Oviducal funnels and large ovaries in XIII ; ovisacs absent. Spermathecal ducts about $\frac{1}{4}$ the length of the large ampulla in VIII and IX ; adiverticulate.

DISTRIBUTION. South America : upper reaches of the Pilcomayo River in exceedingly salt, bitter water.

REMARKS. No specimens of this species are traceable.

***Eukerria kukenthali* (Michaelsen, 1908)**

Fig. 2G–J, 9B–D

Kerria kukenthali Michaelsen, 1908 : 24 ; Michaelsen, 1935 : 102.

Kerria selangorensis Stephenson, 1931 : 279, Fig. 8.

Eukerria peguana Gates, 1942 : 67.

Eukerria asilis Righi, 1968 : 180, Fig. 1–5.

l = 20–70 mm, w = 0.7–1.2 mm, s. = 105–142. Prolobous, proepilobous, or indistinctly epilobous. In the forebody *aa* = 0.75–1 *bc* and more or less than 3 *ab* ;

$ab = cd$; $aa : ab : bc : cd : dd = 4.5 : 1 : 5.8 : 1 : 16$, in the midbody, $= 3.4 : 1 : 3.8 : 1 : 12.2$, in the hindbody ; $dd : u = 0.42-0.44$ ($-0.5?$). Nephropores externally unrecognizable. Clitellum saddle-shaped (?), XIII, $\frac{1}{2}$ XIII, $1/n$ XIII, XIV-XIX, $1/n$ XX, interrupted (or merely weaker?) in aa ; ventral setal couples are present throughout but may be obscured in XVII and XIX. Prostatic pores slightly lateral of setae b , though often appearing median of b lines of segments beyond the limits of the male field owing to contraction of the field with formation of a more or less deep midventral trench which may extend into XVI and XX. Each prostatic pore on a porophore, the median margin of which is in a lines and which does not completely fill its segment longitudinally. Male pores slightly lateral of setae b in seminal grooves, with tumid margins, which connect the anterior and posterior prostatic pores and may be straight or variously bent according to the state of contraction. A sucker like or raised glandular (?) area present midventrally in XXI, almost filling the segment longitudinally and extending laterally of the ventral setal couples the sites of which may be occupied by a papilla on each side and which may be obscured. This genital marking occasionally developed on one side only or absent. Female pores paired, near the anterior margin of XIV, slightly lateral of b lines. Spermathecal pores paired in $7/8$ and $8/9$, in ab lines, each surrounded by a transversely elliptical field which may be somewhat raised, and may fuse with that of the other side.

Septal glands mostly in V ; some in VI or even in VII. Gizzard, in VII, not or only a little wider than the oesophagus, soft, but with muscular layer as much as twice as thick as that of the oesophagus. Calciferous glands pear-shaped, arising ventrolaterally (or laterally?) by short, slender stalks ; central cavity small and irregular, with an epithelial lining of its own, about $1/3-1/4$ of the width of the sac ; blood channels running longitudinally in the thick walls, with, between them rows of cells penetrated by numerous intracellular canaliculi. Intestine commencing in XII (or XIII?). Preseptal nephridial funnels vestigial? Latero-oesophageal hearts in X and XI ; commissures in IX heartlike but only dorso-ventral. Testes and funnels free, in X. Seminal vesicles racemose, in IX and XI. Prostates attaining a length of at least 6 mm, closely and irregularly wound, extending through several (as many as 10) segments posteriorly ; glandular part 65μ wide ; duct lacking muscular sheen, $\frac{1}{2}-1$ mm long, 35μ wide widening to 55μ and becoming more muscular before penetrating the parietes. Genital marking glands stalked, coelomic and tubular ; the duct as long as but slenderer than that of the prostate, translucent and sinuous ; the gland $0.5-1.5$ mm long and much slenderer than the prostate. Ovaries and funnels in XIII. Spermathecae two pairs, entally swollen to form an ampulla equal to or one third of the length of the more or less distinctly demarcated narrower duct. The ampulla sometimes subdivided by folding and in some cases forming a diverticulum-like outpouching. The entire spermathecae bent and twisted ; its length (not extended) ca. 0.3 mm.

DISTRIBUTION. Peregrine on banks of or in streams. West Indies : St. Thomas. Malaya : Selangor (banks of Batu Caves River). Christmas Island (near Java). Burma : Rangoon ; Kungyangon, Thongwa ; Moulmeia ; Wanetchaung ; Myaungmya ; Ptinmana. Brazil : Marajo Island.

MATERIAL EXAMINED. 1 dissected, clitellate type-specimen, St. Thomas, collector Hartmeyer ; Hamburg Museum, V. 7188. 3 clitellate specimens, Christmas Island, Indian Ocean, from banks of a small stream on terraces, collector J. Harrison, 21. i. 1933 ; B.M. (N.H.), 1934. 3. 12. 40/42. Several clitellate "cotypes" of *Kerria selangorensis*, Batu Caves River, Selangor, B.M. (N.H.), 1933. 2. 14. 62/67.

REMARKS. Re-examination of the Christmas Island specimens has revealed the presence of an accessory genital marking in segment XXI which was overlooked by Michaelsen. A marking is not visible in the type-specimen of *kukenthali* but comparison with the Christmas Island specimens gives no reason to doubt Michaelsen's identification of the latter with *kukenthali*. Such a marking is characteristic of *E. asilis* Righi, 1968, the anatomy of which corresponds sufficiently closely with that of *kukenthali* to leave no doubt of its synonymy with the latter. The same genital marking has been observed in a re-examination of the types of *E. selangorensis*, confirming union of this species with *kukenthali* by Michaelsen (1935).

The discovery of genital markings in XXI in *E. kukenthali* also removes the grounds for recognizing *E. peguana* Gates, 1942, which agrees in all respects with *E. kukenthali*. Rounded protuberances from the prostatic porophores observed on re-examination of the Christmas Island material of *kukenthali* are presumably the "clear glands" described by Gates.

Eukerria limosa (Stephenson, 1931)

Kerria limosa Stephenson, 1931 : 312, Pl. 17, fig. 7.

l = 20–28 mm, w = 0.7 mm, s = 95–127. Almost tanylobous. In the anterior segments *aa* = 2 *bc* elsewhere smaller but always > *bc* ; *cd* lateral, *dd* : *u* nearly 0.5. Clitellum XIII or $\frac{1}{2}$ XIII–XX. Prostatic pores immediately lateral to setae *b*, on XVII and XIX, on round papillae, which are separated, longitudinally, by a space of equal width. Seta *a* or *b* sporadically absent in XVII and XIX ; *b* may be absent in XVIII. Male pores, not externally visible, on XVIII midway between the prostatic pores slightly lateral of *b*. Seminal grooves not recognizable. Spermathecal pores in 7/8 and 8/9 approximately midway between *b* and *c* lines.

Pharyngeal glands ending in VII. Gizzard small, in VII, oesophageal musculature there considerably increased but diameter not greatly. Calciferous glands originating posteriorly in IX ; lumen slitlike ; the very thick wall honeycombed by numerous blood spaces separated by stout trabeculae and confluent posteriorly to become fewer and larger. Last hearts in XI. Testes and funnels free in X. Seminal vesicles in IX and XI. Vasa deferentia not terminally thickened. Prostates passing gradually into muscular ducts about 200 μ long which discharge through cushion like thickenings ; terminal bursae absent. Spermathecae with ental portion tubular and twisted, with narrow lumen 6–8 μ or less in diameter ; further ectally a sharply demarcated portion with irregular cavity 20–28 μ in diameter and, finally, a short duct which has an extraordinarily thick muscular sheath ; diameter of spermatheca 34 μ in the ental tubular portion ; 70 μ in the ectal, swollen region.

DISTRIBUTION. Paraguay : Makthlawaiya (mud of shallow pools after rain).

REMARKS. The "cotypes" of this species in the British Museum (1930. 7. 30. 7/13) are all that the author has been able to trace. All are immature or lack the anterior and genital regions.

***Eukerria mcdonaldi* (Eisen, 1893)**

Fig. 9E-F

Kerria mcdonaldi Eisen, 1893 : 294, Pl. XI, fig. 1-6, 8-10, Pl. XII, fig. 13-27 ; Eisen, 1900 : 135 ; Michaelsen, 1900 : 372.

?*Kerria zonalis* Eisen, 1893 : 311, Pl. XI, fig. 7, 11, 12, Pl. XII, fig. 28-30. Michaelsen, 1900 : 372.

l = 25 mm, w = "1 line". All setae present in XVII-XIX, but setae *ab* here $\frac{1}{3}$ smaller and slightly wider than other setae. Most setae with minute cicatrizing at the free ends. Clitellum saddle-shaped, XIII-XX. Male genital field a raised area on each side of the ventral midline, separated by a cylindrical cavity crossing XVII-XIX ; this cavity bridged internally by arciform muscles. Prostatic pores paired in the setal zones of XVII and XIX shortly lateral of setae *b* ; male pores paired in XVIII, each on a small papilla, immediately lateral of setae *b* and therefore slightly median of the prostatic pores. Seminal groove on each side connecting the prostatic pores and curving slightly medially but deflecting a little laterally to skirt the male pore which it does not include. The prostatic pores lying on transversely oblong papillae which are thicker laterally. These papillae and the body wall medial of the seminal groove forming an approximately crescent shaped genital zone on each side. Female pores in front of setae *ab* of XIV. Spermathecal pores paired, in $\frac{7}{8}$ and $\frac{8}{9}$, or in $\frac{8}{9}$ only, in *cd* lines.

Last septal glands in VII ; oesophagus in $\frac{1}{2}$ IV to anterior XII, gizzard very rudimentary in VII. Calciferous glands arising from the oesophagus anteriorly in IX ; hidden by the oesophagus in dorsal view ; each rounded and blunt, with a single internal cavity with large projecting ridges and traversed by longitudinal blood vessels. Intestine commencing abruptly, anteriorly in XII. Gut highly vascularized in XI-XX. Hearts in X and XI. Nephridia commencing in IV ; with peritoneal cells in IX posteriorly ; ducts avascular. Testes and large sperm funnels in X ; unpaired (?) "sperm sacs" or "sperm masses" in X and XI ; seminal vesicles absent from IX. Vasa deferentia superficial on the parietes and very tortuous, ending at the male pores, in XVIII, without terminal dilatation. Exceptionally with a second pair of sperm funnels in XI, and additional seminal vesicles in XII ; the anterior pair of sperm ducts opening adjoining the anterior prostatic pores in XVII, the posterior pair at the male pores in XVIII. Prostates 2 pairs (abnormally double on each side) much bent, when extended about as long as the width of a segment ; glandular part of the anterior and posterior prostates about three times and five times as long respectively as the muscular duct ; ducts of the anterior much narrower than those of the posterior pair ; neither with terminal expansion. Ovaries (palmate) and funnels in XIII ; ovisacs absent. Spermathecae with large, saclike ampulla and narrow tubelike duct, and usually, at their junction, with a diverticulum which is 3-lobed ; spermatozoa stored in the ampulla, not in the diverticula ; the

ampulla usually bent on the duct. The anterior spermathecae usually smaller, never larger, than the posterior pair. Spermatophores [?] paddle-shaped.

DISTRIBUTION. Baja California : Miraflores near San Jose del Cabo (In mud) ; Cape Region (a pond near Santa Ana).

REMARKS. *E. zonalis* agreed with *E. mcdonaldi*, with which the single specimen was collected, in lacking a gizzard, in the location of spermathecal, male and prostatic pores and in the possession of spermathecal diverticula and according to Eisen "much resembles" *E. mcdonaldi*. Differences from *mcdonaldi* were persistence of setae *b* in XVII and XIX, absence of spermathecae from VIII and duplication of the prostate glands on each side. On the whole resemblance to *mcdonaldi* is so close, even to the most unusual possession of spermathecal diverticula, and the chief difference, duplication of the prostate, is so clearly an abnormality that *zonalis* is here regarded as a junior synonym.

Elsewhere in the Ocnerodrilinae spermathecal diverticula are seen only in *Pygmaeodrilus*. There, however, they store sperm as is usual in the megascolecoïds.

The presence in *E. mcdonaldi* of "sperm sacs" in X and XI (Eisen, 1893) was subsequently denied (Eisen, 1900). In the latter account there were said to be only "sperm masses", in X and XI. It seems likely that there were free sperm masses in X and seminal vesicles in XI.

Eukerria papillifera (Rosa, 1895)

Fig. 9G

Kerria papillifera Rosa, 1895a : 3 ; Rosa, 1895b : 145, Pl. fig. 19-21 ; Michaelsen, 1900 : 370.

l = 55-60 mm, w = 2 mm, s = 140. Epilobous. *aa* somewhat smaller than *bc*. Setae ornamented distally by 4-5 longitudinal rows of arcuate depressions. Clitellum saddle-shaped, XIII-XIX, interrupted in *aa* and by the male field. Prostatic pores in *ab* lines on minute papillae in sucker-like depressions on large dome-shaped papillae. Seminal grooves absent. Male pores in XVIII in line with the prostatic pores. Ventral setae present on XVIII, absent from XVII and XIX. 3 unpaired midventral genital papillae in the posterior halves of XIV, XV and XVI. Spermathecal pores large, in setal lines *b*, with tumid lips.

Gizzard absent. Calciferous glands round-based cones. Testes? Prostates tortuous or straight, extending through as many as 20 segments; ducts about 3 segments long each opening through a muscular copulatory sac. Posterior pair of spermathecae larger than the anterior ; ampulla oval, wider anteriorly, with short, wide, sharply demarcated duct, without diverticula.

DISTRIBUTION. Central Paraguay.

REMARKS. Two specimens in Torino Museum (ol. 113, ex. 289) collected by L. Borelli in Central Paraguay, are presumably syntypes but neither possesses the clitellar end.

Eukerria pascuorum (Stephenson, 1931)

Kerria pascuorum Stephenson, 1931 : 316. Pl. fig. 10.

$l = 33-60$ mm, $w = 0.8$ mm, $s = (110?) - 144$. Prolobous. Setae : $aa = 3$ $ab = bc$; $ab = cd$; $dd : u = 0.5$. Clitellum saddle-shaped, XIV-XX and (sections) the greater part of XII. Prostatic pores on XVII and XIX in bc , nearer b than c lines, on small porophores which are carried on moderately large, conspicuous papillae twice as long as wide, occupying the length of their segments and a little of XVIII ; a small part of XVIII equal to the diameter of a papilla intervening between the papillae of a side ; seminal grooves straight. Male pores (in sections) intermediate between and in line with the prostatic pores. Ventral surface of XVIII sometimes tumid. Spermathecal pores (from sections) in $7/8$ and $8/9$ in c lines.

Last septal glands in VII. A moderate gizzard, with thick walls, but not much wider than the oesophagus, in VII. Calciferous glands arising posteriorly in IX ; pear-shaped with broad end anterior ; lumen slit-like or star-shaped, walls honey-combed as in *limosa*. Last hearts in XI. Testes and funnels free in X ; seminal vesicles in IX and XI lobulated or racemose. Prostates extending posteriorly through several segments ; duct equal in diameter to glandular part but muscular. Walls of glandular part one cell thick. Duct equal to or a little more than a segment in length, widening close to its termination at the surface of its porophore but lacking a terminal bursa or special muscular investment. Spermathecal ampulla elongated-ovoid or cylindrical ; sometimes bent on itself and sometimes constricted at the bend ; duct short but so muscular as to equal ampulla in width.

DISTRIBUTION. Paraguay : Makthlawaiya (Mud of ponds in pasture).

MATERIAL EXAMINED. 3 syntypes, immature or lacking the anterior and genital region, excluded from the above description ; B.M. (N.H.), 1930. 7. 30. 51/53.

REMARKS. Distinctions from the sympatric *E. limosa* are few and of doubtful importance. The small lumen of each calciferous gland and the more ventral location of the spermathecal pores appear to separate both species from the otherwise rather similar *E. eiseniana*.

Eukerria rosae (Beddard, 1895)

Fig. 4A-F

Kerria rosae Beddard, 1895 : 224 ; Beddard, 1896 : 41 ; Michaelsen, 1900 : 372 ; Pickford, 1928 : 381, Fig. 5.

$l = 25-35$ mm, $w = 1-1.2$ mm, $s ?$. Setae closely paired ; in segment XII $aa : ab : bc : cd : dd = 2.8 : 1 : 3.4 : 0.81 : 10.6$; $dd : u = 0.45$ (1 type-specimen, B. M. (N.H.)) ; setae a present on the male field, b present or absent. Nephropores conspicuous small papillae anteriorly in their segments about $1/3$ bc below c lines or (Hamburg material) not visible. Clitellum imperfectly developed. Prostate pores on small papillae nearer b than c , on XVII and XIX, each surrounded by a low, laterally elevated auricular lobe limited to its segment ; the 2 pores of a side connected by a seminal groove which is only slightly bent medianwards, and is bordered by slightly

tumid ridges. Male pores not externally apparent, from internal examination, in the seminal grooves at mid XVIII. Female pores on small circular papillae anterior in XIV, slightly lateral of *b* lines. Spermathecal pores inconspicuous, bordered anteriorly and posteriorly by slight ridges or on small papillae, about one-third *bc* below setal lines *c*.

Last septal glands in VII. Gizzard barely twice the width of the oesophagus but

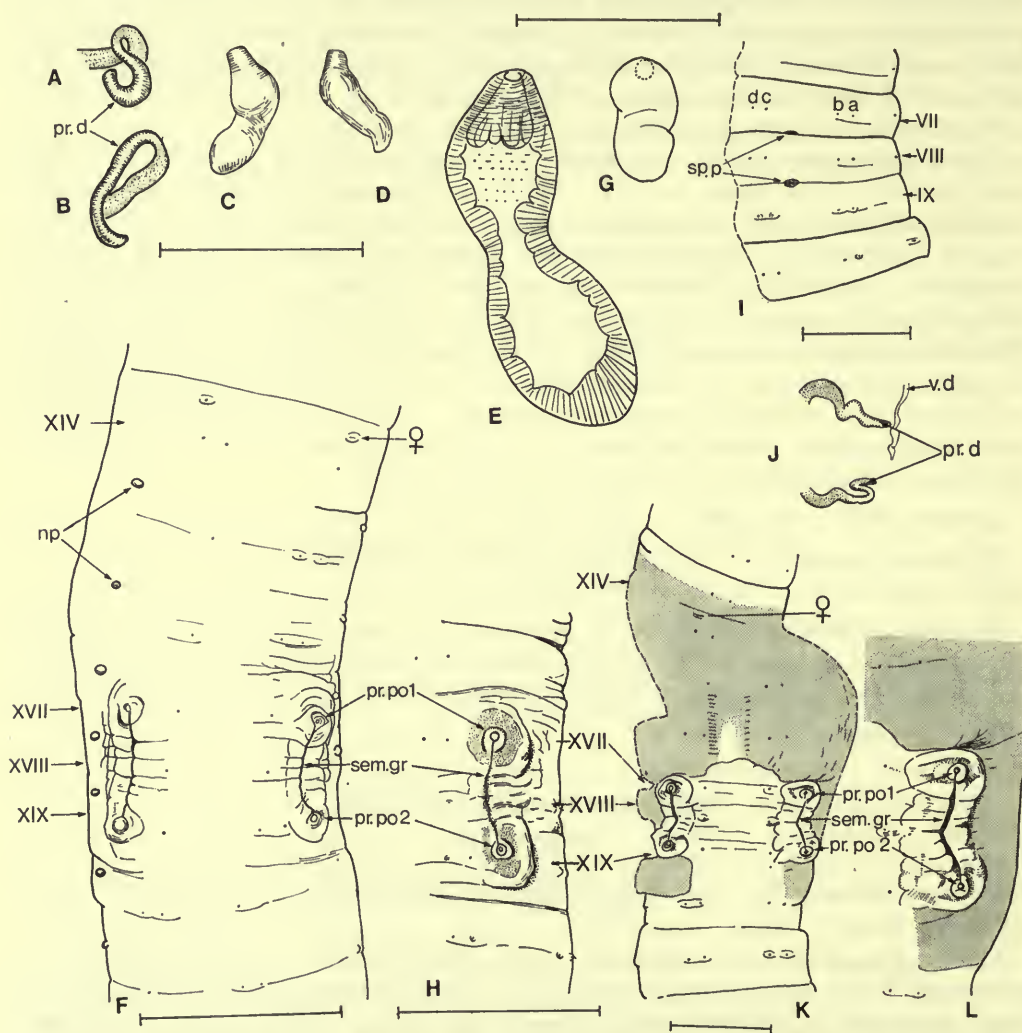


FIG. 4. A-F. *Eukerria rosae*, syntype, B.M. (N.H.), 1904.10.5. 929 : A and B, right anterior and posterior prostates ; C and D, left posterior and right anterior spermathecae respectively ; E, former spermatheca cleared (freehand) ; F, male genital field. G-H, syntype, Hamburg Museum, V. 4103 : G, left spermatheca of VIII ; H, male genital field of left side of same. I-L, *E. saltensis*, syntype, B.M. (N.H.), 1904.10.5. 928 : I, spermathecal pores ; J, prostates ; K, clitellar region ; L, left side of same.

firm and thickly muscular. Calciferous glands almost sessile stoutly pear-shaped, broad end anterior, adpressed medianly below the oesophagus beyond which they project laterally. The walls of each pouch fairly thick, permeated by blood vessels, and projecting in places as folds into the lumen. Intestinal origin in XII; oesophageal valve well developed at approximately $\frac{1}{2}$ XII. Typhlosole absent. Last hearts, in XI, exceedingly large, those in X less so. Nephridia aversiculate, the first in VII. Proandric; sperm funnels multilocular, in X; seminal vesicles in IX and XI; sperm ducts slightly widened in XI. Prostates extending posteriorly into XXIII. Glandular parts exceedingly long; except ectally, thread-like and much coiled and mutually entangled; maximally $90\ \mu$ wide. Ducts muscular and glossy, gently curved or strongly sigmoid, $40\text{--}90\ \mu$ wide and approximately 0.7 mm long; lacking terminal expansions. Spermathecae $0.6\text{--}0.7\text{ mm}$ long; the duct muscular, approximately one sixth of the length of the ampulla. Ampulla digitiform, wider ectally.

DISTRIBUTION. Argentina: Buenos Aires (Barracas do Sul, under stones, on the banks of a river).

MATERIAL EXAMINED. 5 semimature syntypes, Buenos Ayres, Beddard collection, B.M. (N.H.) 1904. 10.5. 929/33. Many semimature syntypes, Buenos Ayres, "Barracas d. Sul, Fluss Ufer" collector Michaelsen, 26. VII. 1893, Hamburg Museum, V. 4103.

REMARKS. Re-examination of the specimens in the British Museum permits the above very considerable extension of previous accounts. *E. rosae* is morphologically and probably cladistically very close to *E. saltensis* but is clearly distinguished by the very short spermathecal ducts and ectal widening of the ampullae. Conspicuous nephropores distinguish the British Museum material from *E. saltensis*, in which none of the many specimens which have been described possessed visible pores, but nephropores are not recognizable in the many Hamburg Museum specimens. As the specimens in both museums are labelled as types it seems possible that differences in the method and condition of preservation have resulted in the difference in visibility of the pores.

Only a brief examination of the Hamburg specimens has been possible, little being observed beyond the form of the spermathecae, wider ectally than entally with an extremely short duct, and the form of the male genital field.

Eukerria rubra (Friend, 1916)

Kerria rubra Friend, 1916: 147, Fig. 1-6.

$l = 38\text{ mm}$, $w = 2\text{ mm}$, $s = 90$. Setae: *dd* less than $0.5\ u$. Clitellum saddle-shaped, XIII-XX. Prostatic papillae inconspicuous, on XVII and XIX. Male pores on XVIII, not in line with the prostate pores. Spermathecal pores 2 pairs, in $7/8$ and $8/9$, in *cd* lines (also said to be immediately below *c*).

Septal glands extending between IV and VIII. Gizzard absent. Calciferous glands pear-shaped, arising laterally and disposed ventrolaterally; apparently with

a rather narrow lumen and thick walls. Intestinal origin in XII. Nephridia commencing in VII ; absent from segments XI and XIV. Testes and funnels (free?) in X ; seminal vesicles in IX and XI. Vasa deferentia apparently lacking terminal dilatation. Prostates with glandular part lined by a single layer of cells, extending at least to XXI ; ducts short, approximately equal in length to a segment ; lacking terminal bursa. Ovaries and funnels in XIII ; ovisacs in XIV. Spermathecae "pear or bottle-shaped" with slightly swollen ampullae ; and slightly longer, fairly sharply demarcated, tubular ducts about half as wide.

DISTRIBUTION. Focus of endemicity unknown. Type-locality the Lily House, Oxford Botanical Garden, England, "in oozy mud which surrounded the plants on one side of the tank".

REMARKS. The description of this species, specimens of which are no longer traceable, is inadequate and it probably should be regarded as a *species dubium*.

Eukerria saltensis (Beddard, 1895)

Fig. 4I-L, 9J,K, 10D

Kerria saltensis Beddard, 1895 : 225 ; Beddard, 1896 : 42 ; Michaelsen, 1898 : 479 ; 1900 : 371 ; 1904 : 286 ; 1907 : 23 ; 1935a : 103 ; 1935b : 40 ; Pickford, 1928 : 378, Fig. 1-4 ; Gates, 1942 : 73 ; Gavrilov, 1952 : 692 ; Jamieson, 1967 : 61, Fig. 1.

Acanthodrilus sydneyensis Sweet, 1900 : 124, Pl. 14, fig. 7, Pl. 15, fig. 18.

Kerria gunningi Michaelsen, 1913b : 1, Fig. 1 ; Michaelsen, 1913c : 419 ; 1913e : 276.

?*Kerria nicholli* Jackson, 1931 : 121, Pl. XVI, fig. 5, 8, 9, 11.

l = 25-100 mm, w = 1-2 mm, s = 118-135. Epilobous. In segment XII, *aa* ca. = *bc*, *ab* = *cd*, *dd* : *u* = 0.35-0.39 (-0.5?) ; in the type (postclitellar) *aa* : *ab* : *bc* : *cd* : *dd* = 4 : 1.0 : 4.4 : 1.0 : 10.9 ; *dd* : *u* = 0.39. Setae *a* present throughout the clitellum ; setae *b* present or absent in XVII-XIX ; lateral (and ventral?) setae in the forebody bearing minute teeth. Clitellum annular but less tumescent ventrally, $\frac{1}{2}$ XIII, (XIV)-(XIX), ($\frac{1}{2}$ XX, XX), $\frac{3}{4}$ XX (= 7-8 segments). Prostatic pores on minute papillae, on XVII and XIX, considerably lateral of setal lines *b* of adjacent segments ; those of a side connected by a seminal groove with tumid margins which bends medially in XVIII in which it contains the male pore (i.e. male pores considerably mediad to the prostatic pores but still lateral of *b* lines). Each prostatic papilla encircled by the groove and situated on the summit of a transversely oval prominence which is not clearly defined medially and is in turn borne on a low, earlike prominence which is only laterally elevated. Nephropores not visible externally. Female pores conspicuous or not, anterior in XIV, in *b* lines, or much less commonly in *ab* lines or lateral of *b* lines ; on minute cones or with narrow lips. Spermathecal pores in $\frac{7}{8}$ and $\frac{8}{9}$, mostly at $\frac{2}{3}$ *bc*, occasionally at mid *bc* ; usually readily observed on close examination but never conspicuous.

Last septal glands in VI. Gizzard weakly to well developed in VII. Calciferous glands slenderly pear-shaped rather thick walled, permeated by blood vessels (and intracellular spaces?) but without internal folds. Intestine commencing in XII. Hearts 3 pairs ; latero-oesophageal in X and XI ; dorsoventral in IX. Nephridia

commencing in VI (?), entering the parietes at mid *bc* (with small terminal dilatation of the duct?). Testes and funnels large, free, in X. Seminal vesicles in IX and XI or XI only. Prostates very slender (0.06–0.1 mm wide), winding posteriorly into XXVI or further; ducts slightly or much more slender, demarcated by their muscular sheen. Neither prostatic nor sperm ducts notably thickened ectally. Ovaries (palmate) and funnels in XIII; ovisacs absent. Spermathecal ampulla large and oblong-ovoid with thin walls; duct (always?) with a capacious thin walled ental chamber approximately one third the length of the ampulla, and a muscular terminal portion which is as long as, or shorter than the remainder. Total length of spermatheca 0.5–0.8 mm.

DISTRIBUTION. South America : Chile ; Juan Fernandez Is ; Argentina. South Africa : Cape Province ; Natal ; Transvaal-Orange Free State border. Burma. New Caledonia. Australia : New South Wales ; S. West Australia (?) ; Queensland.

MATERIAL EXAMINED. A single fragmentary previously dissected clitellate type-specimen of *K. saltensis*, Beddard collection, B.M. (N.H.), 1904, 10.5. 928. A clitellate type-specimen of *Kerria gunningi*, Hamburg Museum, v. 7490.

REMARKS. This is the most widely peregrine species of *Eukerria*.

The type-specimen in the British Museum now yields little information beyond what is indicated in the accompanying illustrations. The prostomium is epilobous $\frac{1}{2}$, closed acute; setal ratios are as recorded above; nephridia enter the parietes slightly above mid *bc* and have each a very small ectal dilatation of the duct; the gizzard is about twice the width of the oesophagus but strongly muscular; the spermathecae have been severed shortly ental to the duct which is muscular and spindle-shaped; and the prostates are much coiled and extend to XX.

I follow Pickford (1928) in including the South African *K. gunningi* as a junior synonym of *E. saltensis*. A Hamburg Museum specimen differs from the type of the latter taxon in having a long U-shaped muscular spermathecal duct (the knoblike ampulla being one fourth of its length) but that illustrated by Pickford showed the usual *saltensis*-form and there is no evidence to suggest that the variation observed is not intraspecific. A large number of specimens from South Africa described by Jamieson (1967) accord closely with the type and with Beddard's descriptions of it.

Eukerria stagnalis (Kinberg, 1867)

Fig. 5, 6, 10C

Mandane stagnalis Kinberg, 1867 : 100.

Acanthodrilus stagnalis ; Vaillant, 1899 : 177.

Kerria stagnalis ; Michaelsen, 1899 : 426 ; 1900 : 370.

Eukerria stagnalis ; Cordero, 1942 : 278, Fig. 8.

Acanthodrilus spegazzinii Rosa, 1890 : 516, 1 Fig.

Kerria spegazzinii ; Rosa, 1895b : 146 ; Beddard, 1896 : 40.

l = 31–86 mm, w = 0.8–3 mm, s = 80–168. Prostomium epilobous $\frac{1}{2}$, sometimes $\frac{3}{4}$, usually open. Pigmentless in alcohol. Setae closely paired. In segment XII :

		<i>aa</i>	<i>ab</i>	<i>bc</i>	<i>cd</i>	<i>dd</i>	<i>dd : u</i>
Buneos Aires	{ large morph	4.0	1.0	5.6	0.8	18.6	0.50
		3.2	1.0	4.0	0.9	15.5	0.51
	{ small morph	3.2	1.0	4.6	1.0	15.6	0.49
Paraguay	{	5.6	1.0	6.8	1.2	16.2	0.41
		4.6	1.0	6.4	1.2	20.4	0.49
mean of 5		4.1	1.0	5.5	1.0	17.3	0.48

Setae *a* present, *b* present or absent in XVIII, totally absent in XVII and XIX ; penial setae absent. Nephropores rarely visible as white dots shortly median of setae *c*. Clitellum annular though interrupted by the male genital field, occupying XIII $\frac{1}{2}$ XIII-XIX, $\frac{1}{2}$, $\frac{2}{3}$ XX (= $6\frac{1}{2}$ - $7\frac{2}{3}$ segments) ; ventrally less strongly developed and sometimes embayed almost to $\frac{1}{2}$ XIV ; intersegmental furrows present only ventrally, setae retained. Male genital field : prostatic pores two pairs of conspicuous transverse gaping slits, in XVII and XIX, wider than a setal couple, their centres in line with the ventral setal couples of neighbouring segments ; a single or double conical penis-like structure may be visible projecting through a pore. Each pore almost spanning a low oval papilla which is surrounded by a broad low tumid area which extends laterally to almost mid *bc*, fills the segment longitudinally and is united with those of the other side. Male pores a pair of small, rarely visible slits, on XVIII, shortly lateral of, less commonly at the sites of, setae *b* ; the ventral couples often translocated medially ; bordered by tumid longitudinal bands, confluent or contiguous medially, which are continuous with the tumid prostatic fields. Seminal grooves indistinct tracts connecting the prostatic and male pores of each side or not distinguishable their courses varying according as the male pores are median to, in line with, or lateral to the prostatic pores. Glandular mounds, approximately as large as the prostatic porophores, present in line with or median to the latter postsetally in XVI and presetally in XX, or vestigial or absent, surrounded by tumid areas confluent with the male genital field.

Female pores inconspicuous, shortly lateral of *b* lines anteriorly in XIV. Spermathecal pores 2 pairs of transverse slits with slightly raised margins, in $7/8$ and $8/9$, their centres in or slightly lateral of *b* lines. Dorsal pores absent.

Pharynx in III, invested by lobulated pharyngeal glands which extend to the anterior region of VI. Gizzard totally absent. Calciferous glands ; broadly pyriform, narrowing posteriorly to a short duct which joins the lateral aspect of the oesophagus ; the two glands contiguous or nearly so below the oesophagus. The walls thin, with approximately twelve thick vascularized radial septa projecting into the lumen for varying distances, some uniting with neighbouring septa or with those of the other side or all free ; walls and septa ciliated. Intestine beginning, with abrupt expansion, in XII ; typhlosole absent. Dorsal blood vessel slender in the region between the pharynx and the posterior hearts, not certainly traced onto the pharynx. Dorsoventral commissural vessels in (V?), VI-XI ; those in X-XI forming latero-oesophageal hearts, receiving connectives from the dorsal and supraoesophageal vessels. Supra-oesophageal vessel as wide as or much narrower than the dorsal

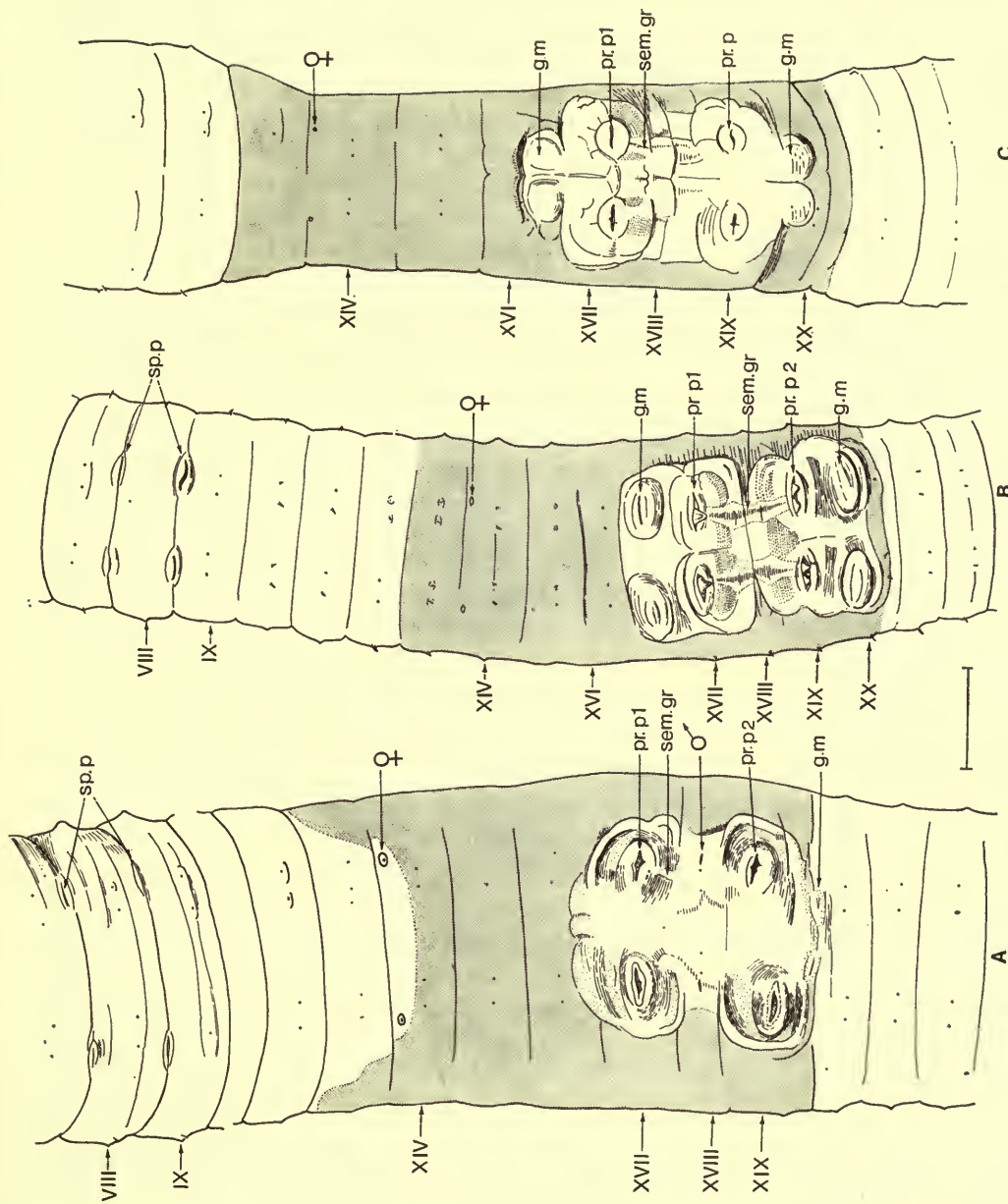


FIG. 5. *Eukerria stagnalis*, genital fields. A, syntypes of *Kerria spegazzini*, Torino Museum, ol. 114, ex. 291 : A, large morph ; B, small morph ; C, "*Kerria*", Hamburg Museum, V. 6713.

vessel, arising anteriorly as a vessel (calciferous vessel) from each calciferous gland, and ending by bifurcation to form the connectives to the hearts of XI; the calciferous vessels apparently in one specimen giving connectives to the hearts of IX. Calciferous gland on each side supplied apically by a longitudinal latero-oesophageal vessel which is separate from the oesophagus but median to the hearts (traced in VI to IX). Subneural vessel absent. Nephridia stomate holonephridia throughout, the first postseptale in III; (always?) absent from XIV–XVI; ducts avesiculate though not especially narrowing. Dense villiform testes, large anterodorsally directed iridescent funnels and sperm masses in X only, enclosed in a delicate circumoesophageal testis-sac which encloses also the hearts and nephridia.

Very large dorsally apposed racemose seminal vesicles in XI, attached to its anterior septum; smaller, much-dissected seminal vesicles in IX attached to its posterior septum. Prostates 2 pairs, the tubular glandular portion slightly depressed, tortuous, and extending posteriorly through many segments; their ducts with a muscular sheen and continuous with the glands by a non-glossy transitional region. Each duct ending ectally at the postero-dorsal aspect of a large muscular hemispheroidal bursa. Widths of the bursae 0.38–0.78 mm (see Remarks). Vasa deferentia united on each side and ectally expanded to form an approximately fusiform or subspherical bursa; the expansion sometimes extending for much of the length of a segment. Ovaries paddle-shaped laminae composed of linear series of oocytes. Female funnels large and compact; ovisacs absent. Spermathecae inflated sacs each usually once bent on itself and with a firmer ectally narrowing, usually poorly demarcated duct which is from a quarter to a half as long as the saccular ampulla; diverticula absent; total length of a spermatheca of IX 0.9–2.0 mm (see Remarks).

DISTRIBUTION. Uruguay: Montevideo (type-locality). Argentina: Buenos Aires. Brazil: Rio Grande do Sul, Porto Alegre. (Limnic).

MATERIAL EXAMINED. 11 clitellate syntypes of *K. spegazzini* of which 1 large and 1 small specimen were dissected; Buenos Aires, collector L. Borelli, 1893, Torino Museum, ol. 114, ex. 291. 3 clitellate specimens of "*Kerria*" of which 1 was dissected, N. Paraguay, collector? Hamburg Museum, V. 6713.

REMARKS. The existence of infraspecific morphs in *E. stagnalis* poses interesting problems. It appears unlikely that the large morph from Buenos Aires is capable of pairing with the exactly sympatric small morph and the series of both is sufficiently large to cast doubt on the existence of specimens of intermediate size in the neighbourhood. On the other hand the Paraguayan specimens are intermediate in size between the two morphs, their intermediate nature being reminiscent of central populations in a Rassen-Kreis. Additional evidence for the distinctness of the large and small Argentinian morphs is the vestigial nature of accessory markings in the former which are well developed in all 6 clitellate specimens of the small morph and in the 3 clitellate specimens of the Paraguayan morph examined. It is to be hoped that comparisons of ploidy in the three morphs will be undertaken.

Comparative data on the three morphs from the small series available are recorded below. Data are limited as several specimens are posterior amputees or

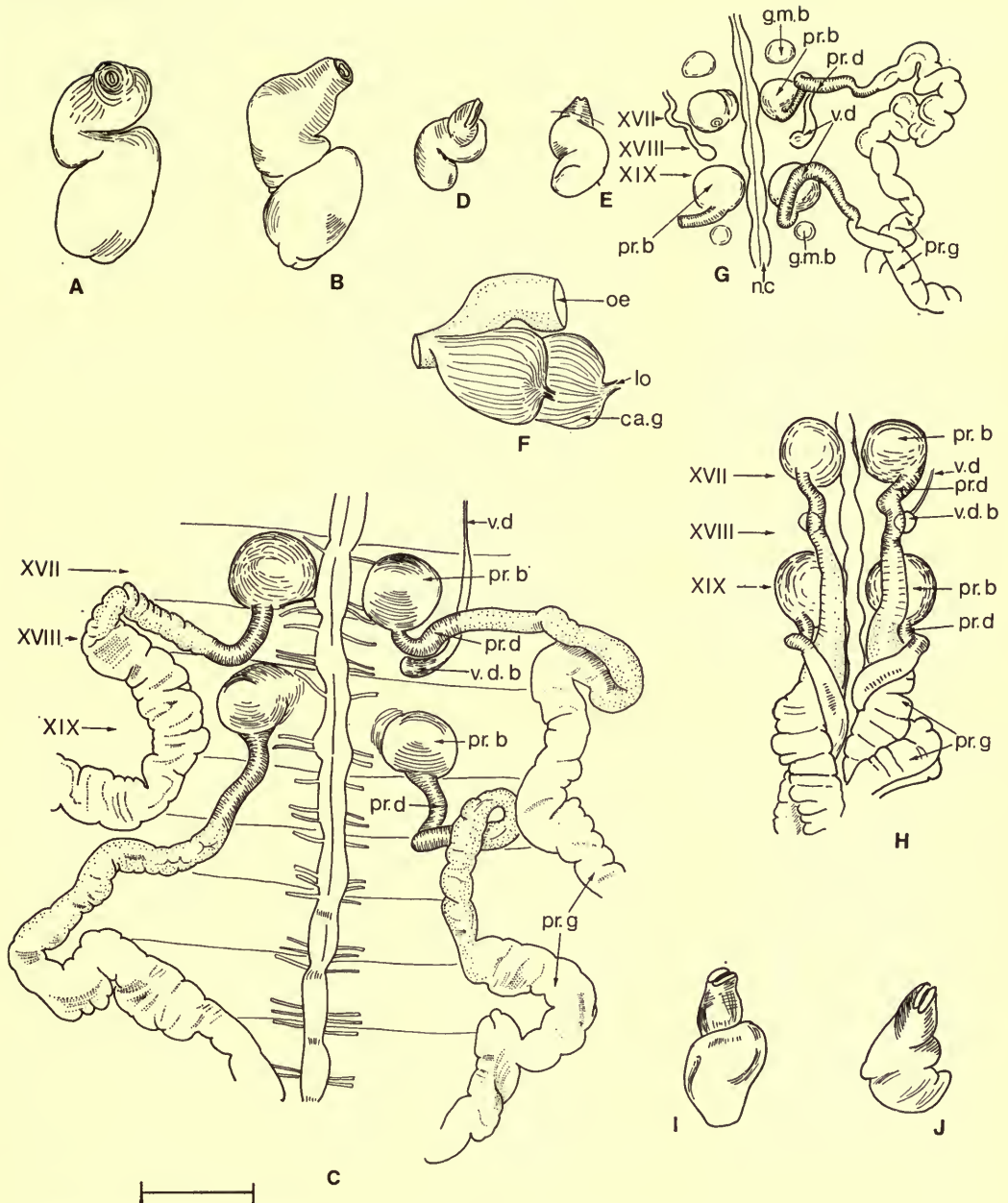


FIG. 6. *Eukerria stagnalis*. A-G, syntypes of *Kerria spegazzini*, Torino Museum, ol 114, ex. 291: A-C, large morph, A and B, ventral and lateral aspects of right spermatheca of IX; C, prostates of same specimen. D-G, small morph, D and E, median and dorsal aspects of left spermatheca of IX; F, lateral view of calciferous glands; G, prostates of same specimen; H-J, "*Kerria*", Hamburg Museum, V. 6713, H, prostates; I and J, ventral and lateral aspects of right spermathecae of VIII and IX. (All to same scale).

regenerates and because of the desirability of minimizing dissection. Numbers of specimens examined are shown in parentheses. Measurements are in mm.

	Small morph	Large morph	Paraguayan morph
Length	31-52 (6)	82-86 (2)	62-82 (3)
Greatest width	0.8-1.1 (6)	1.5-1.9 (3)	2.5-3 (3)
Mid-clitellar width	1.8-2.4 (mean of 4 = 2.1)	3.1-4.4 (mean of 4 = 3.5)	2.1-2.4 (mean of 3 = 2.3)
Segments	80-123 (6)	168-170 (2)	88 (regenerating?)— 154 (3)
Accessory genital markings	Well developed (6)	Vestigial (3)	Well developed (3)
Width prostatic bursae	0.38-0.47 (1)	0.69-0.78 (1)	0.59-0.69 (1)
Length of a spermatheca in IX	0.9 (1)	2.0 (1)	1.2 (1)

The greater width of the Paraguayan specimens appears to be due to contraction of the forebody, the clitellar width being intermediate between that of the other two morphs.

Eukerria subandina (Rosa, 1895) emend. Gavrilov, 1967

Fig. 7, 8, 9H, I, L, 10E

Kerria subandina Rosa, 1895a : 2 ; Rosa, 1895b : 143, Pl. fig. 17, 18 ; Michaelsen, 1900 : 371 (Including *K. borellii*) ; Cognetti, 1902 : 3 ; Pickford, 1928 : 381, Fig. 7.

Kerria borellii Cognetti, 1900 : 6, Pl. fig. 6 ; Cognetti, 1902 : 3 ; Pickford, 1928 : 381, Fig. 8 ; Gavrilov, 1967 : 144, Fig. 1-7.

l = 30-81 mm, w = 1.4-2.4 mm, s = (76?) 100-136, rarely 148-169. Rosy in life. Proepilobous to epilobous. Setae narrowly ornamented from segment II. Setae *ab* absent or only partly represented in XVII-XIX ; *ab* = *cd* (or larger or smaller) ; *dd* : *u* = 0.5 or rarely somewhat smaller. In a type of *borelli*, in XII, *aa* : *ab* : *bc* : *cd* : *dd* = 3.5 : 1.0 : 4.4 : 0.63 : 1.43 ; *dd* : *u* = 0.47. Nephropores (always?) in *bc* near *c* ; in the preclitellar segments in front of *c* ; in the postclitellar segments further presetally. Clitellum annular, less developed ventrally and interrupted by the male genital field ; in XII, $\frac{1}{2}$ XII, $\frac{1}{n}$ XII, -XII, XIII-XIX, $\frac{1}{2}$ XX, $\frac{2}{3}$ XX, $\frac{3}{4}$ XX, XX (=7-9 segments). Male genital field I-shaped, ventral median between the equators of XVII & XIX ; its angles reaching transversely a variable distance into *bc* ; its median region less extensive, generally not extending above *ab*. The four prostatic pores central or eccentric on transversely elongated or round papillae, which extend in the angles of the male field, from *b* laterally. Seminal grooves, with more or less elevated and whitish margins, convex towards the mid-ventral line, reaching to or approximately to *a* ; male pore at the bottom of each groove, at the equator of XVIII with a tendency to be very slightly lateral of *a*. Prostatic papillae and the areas delimiting them, joining the elevations of the seminal grooves, constituting little-developed porophores which laterally delimit the male genital field ; the area median to these, with anterior and posterior margins of variable configuration, may be prominent, level with the remainder of the integument, or depressed. In several re-examined syntypes of *borelli* there is a pair of pad-like accessory genital markings at 19/20, sometimes represented on one side only or

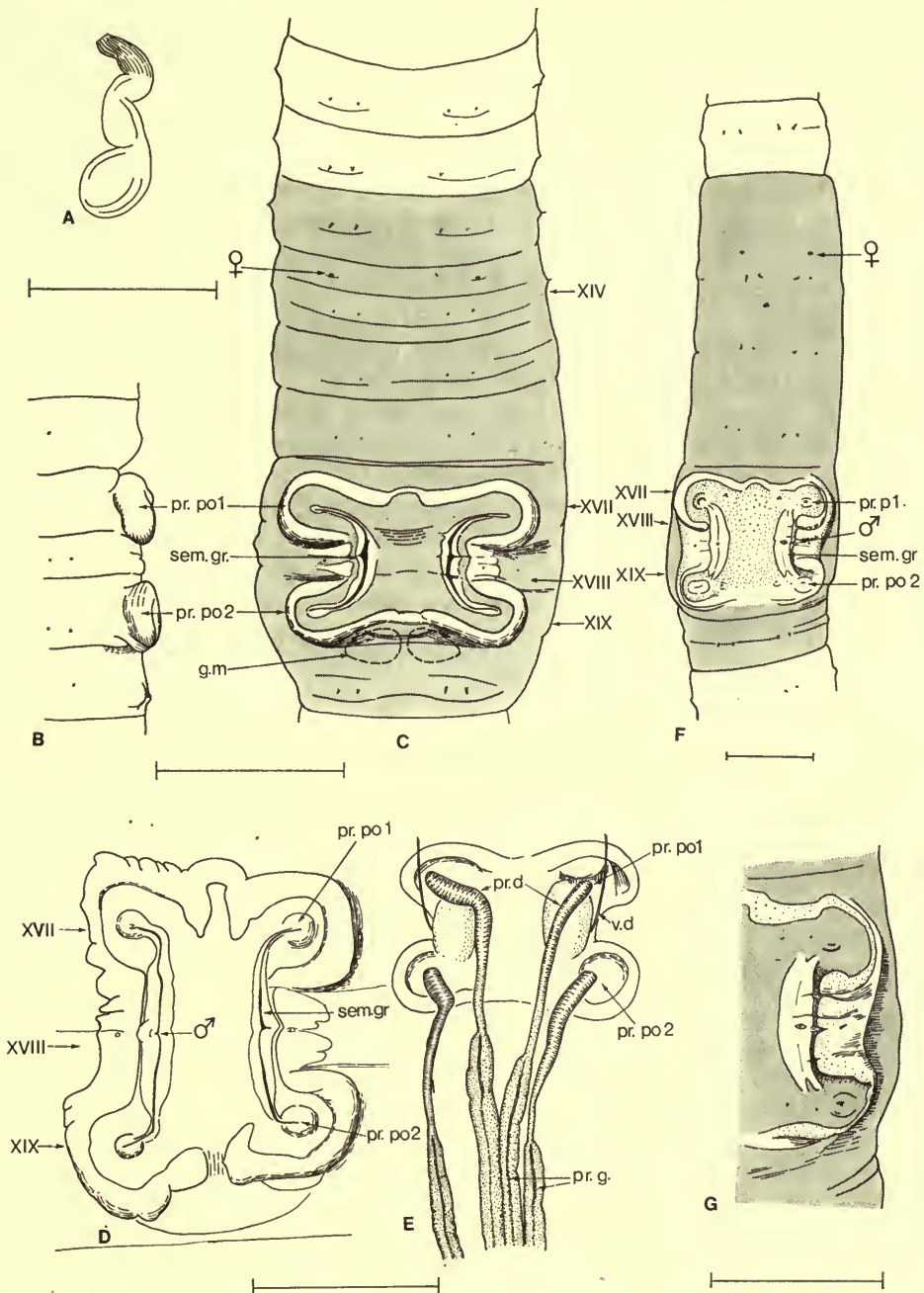


FIG. 7. *Eukerria subandina*. A-E, syntypes of *Kerria borelli*, Torino Museum, ol. 115, ex. 467: A, right spermatheca of VIII; B, lateral and C, ventral views of the male genital field of the same specimen; D, previously excised male genital field of another specimen; E, prostates of first specimen. F and G, syntype of *K. borelli*, Hamburg Museum, V. 5896: male genital field.

absent. Female pores at the anterior margin of XIV, a certain distance behind 13/14, in or lateral to *b* lines. Spermathecal pores inconspicuous or on papillae, in 7/8 and 8/9, at mid *bc* or as far dorsally as *c* lines.

Last septal glands in VI or VII. Gizzard relatively well developed, in VII ; its muscular coat 3–5 times as thick as the internal epithelium. Calciferous glands (re-examination of the type of *borelli*) with thick walls traversed by longitudinal blood sinuses, which occupy the entire width of the walls, between which are narrow canaliculi which probably are continuous with the central lumen ; septa absent ; structure similar in a type of *subandina*. Intestine beginning in XII, generally at 11/12 ; typhlosole absent. Dorsal and ventral vessels single ; supraoesophageal from anterior XI to posterior IX ; subneural and extraneurals absent. Hearts in IX–XI ; lateral in IX ; laterooesophageal in X & XI ; dorsoventral commissurals seen in VIII, in one syntype of *borelli*, but absent from VII. Nephridia from V (occurring at least as far forward as VI in a re-examined syntype), peritoneum highly developed from the beginning of the clitellum. Testes free ; seminal vesicles racemose, 2 pairs, in IX & XI. Prostates 2 pairs, tubular, convoluted and folded, extending backwards to XXI–XXXVII. Ducts much thinner than and well differentiated from the glandular parts, relatively short, equivalent in length to 1½–2 segments. Ovaries and funnels in XIII ; ovisacs (sometimes rudimentary or absent) in XIV. Spermathecae adiverticulate, claviform, digitiform or inverted pyriform, with a thick, relatively short duct (¼–½ of the length of the ampulla) ; length of the right spermatheca of IX in a re-examined syntype = 1.1 mm ; of the right spermatheca of VIII in a re-examined syntype of *borelli* = 1.0 mm.

DISTRIBUTION. Argentina. Bolivia. Brazil.

MATERIAL EXAMINED. 5 clitellate syntypes of *K. subandina* (1 lacking the preclitellar portion) of which 1 was dissected, Salta, Argentina, collector L. Borelli, 1893 ; Torino Museum, ol. 115, ex. 467. 8 clitellate syntypes of *Kerria borelli* of which 1 was dissected, Urucum, Matto Grosso, Brazil, collector L. Borelli, 1899 ; Torino Museum, ol. 106, ex. 497. 1 clitellate syntype of *K. borelli* (same locality data) ; Hamburg Museum, v. 5896 (not dissected).

REMARKS. After a careful examination of new material from Arroyo del Toro, Province of Tucuman, Argentina, Gavrilov (1967) accepted the suggestion of Michaelsen (1900) that *E. borelli* is a synonym of *E. subandina*. He demonstrated uniparental reproduction in this species. The writer's examinations of type-material of both taxa have yielded no evidence which invalidates regarding *borelli* as a junior synonym and variation falls in every detail within that indicated in the synoptic description of Gavrilov (1967) summarized above. Accessory genital markings noted unilaterally or on both sides in 19/20 in five of six Torino syntypes were not, however, described by Gavrilov. The markings were absent, or perhaps represented by a medianly continuous slight rim or pad, in one of the six specimens and in the Hamburg Museum specimen. The albeit inconsistent occurrence of these markings and the conspicuous appearance of the spermathecal pores confirmed in the re-examination both contrast with the condition in Argentinian specimens and the possibility of subspecific distinction of Brazilian populations deserves investigation.

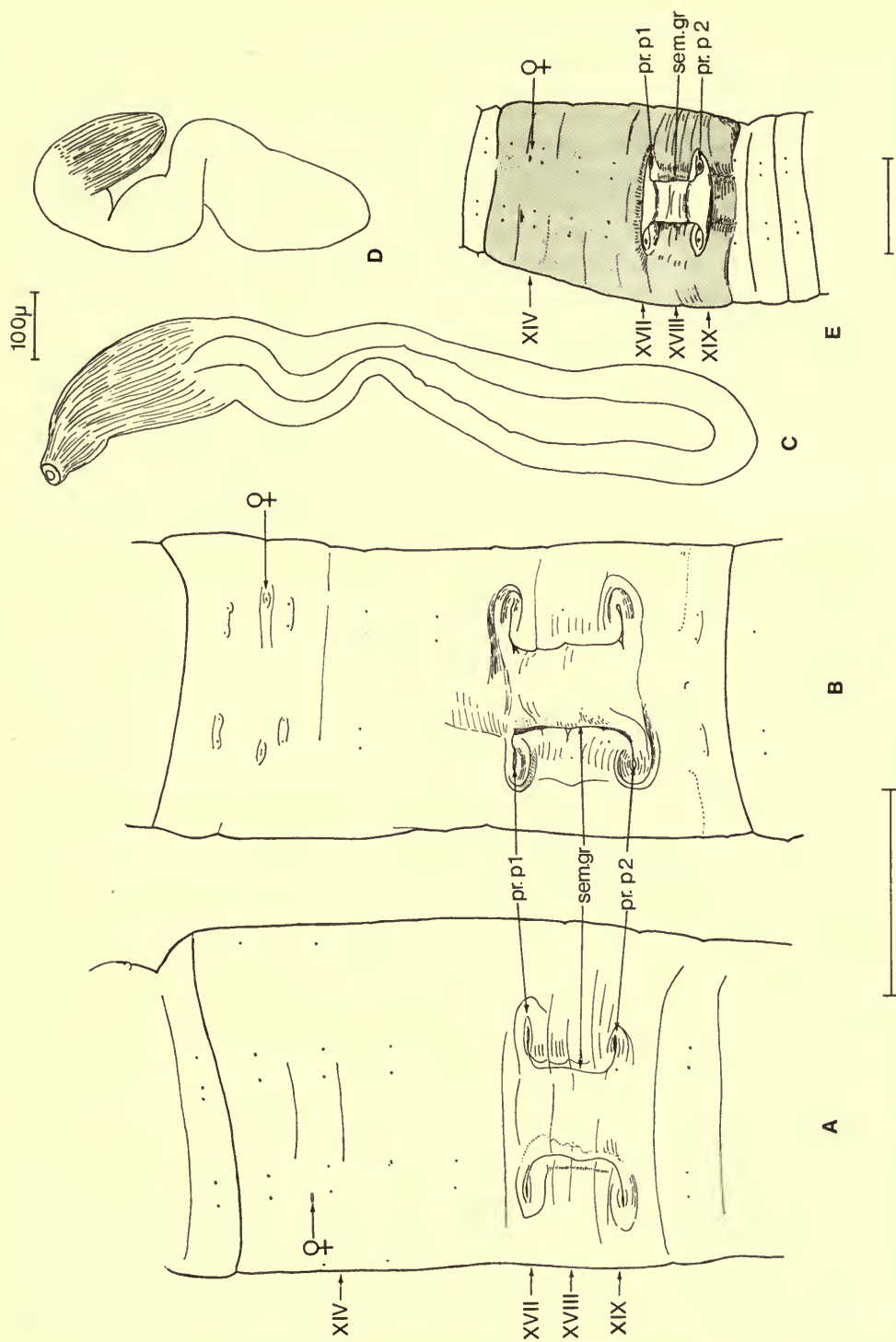


FIG. 8. *Eukerria subandina*, syntypes, A-D, Torino Museum, or. 115, ex. 467 : A and B, male genital fields of two specimens ; C and D right spermathecae of IX and VIII respectively ; E, Hamburg Museum, V. 5894, male genital field.

Eukerria tucumana Cordero, 1942

Fig. 9M, N

Eukerria tucumana Cordero, 1942 : 281, Fig. 12-15.

$l = 63-65$ mm, $w = 1.5-2$ mm, $s = 105-120$. Epilobous. Setae : $ab = cd$; aa less than bc anteriorly, $= bc$ posteriorly ; $aa = 4.5-5 ab$ and $dd > 0.5 u$, especially in the anterior portion. Nephropores in bc , nearer c . Clitellum saddle-shaped, XIII-XIX, $\frac{1}{2}$ XX. Male genital field between XV and XX which region is depressed and concave. 2 pairs of oval tubercles in the most depressed region (XVII-XX), traversed longitudinally by seminal grooves the borders of which are strongly tumid, especially laterally ; prostatic pores in the setal arcs of XVII and XIX slightly lateral of setae b , at the ends of the seminal grooves, on simple papillae which do not project markedly ; the seminal grooves linking these with the male pores, which are in the same longitudinal line at the middle of XVIII which is much extended and depressed. Each pair of tubercles crossed transversely by the intersegmental furrows bordering segment XVIII so that one third lies in XVIII. Female pores anterior in XIV, anteromedial to setae b . Spermathecal pores in $\frac{7}{8}$ and $\frac{8}{9}$, in b lines, recognizable by a slight increase in the parietal pigmentation in their vicinity.

Last septal glands in VI. Gizzard well developed ; at 1 mm wide, much wider than the oesophagus. Calciferous glands arising dorsally from the oesophagus ; with long curved ducts ; the sacs below the gut ; as in *Ocnerodrilus* with small parietal septa. Intestine commencing in XIII. Testes and funnels in X, (free?) ; seminal vesicles racemose, in IX and XI. Prostates extending to XXIX, very attenuated ; their ducts more slender, a little more than the length of a segment ; without terminal expansions. Ovaries in XIII. Spermathecal ampulla triangular, its apex continuing without constriction as a long, wide, coiled duct.

DISTRIBUTION. Argentina : Tucuman. (Habitat?).

REMARKS. *E. tucumana* shows affinities with *E. pascuorum* and *E. eiseniana*.

Eukerria urna Righi, 1968

Fig. 90

Eukerria urna Righi, 1968 : 183, Fig. 6-8.

$l = 22.7-28.4$ mm, $w = 1.23-1.41$ mm, $s = 76-89$. Zygolobous. Reddish pink in life. Setae sigmoid with small, irregularly arranged longitudinal furrows ; $aa : ab : bc : cd : dd = 5.3 : 1.0 : 6.7 : 1.0 : 14.3$, in the midbody, $= 3.1 : 1.0 : 4.2 : 1.1 : 8.6$, in the hindbody ; $dd : u = 0.39$ and 0.35 respectively (computed as 0.5 by Righi). Nephropores not visible. Clitellum annular, less developed ventrally, $\frac{1}{2}$ XIII, $\frac{1}{2}$ XIV- $\frac{1}{2}$ XX. Prostatic pores small transverse slits on pointed, mamillate elevations on XVII and XIX in setal lines b or slightly above these ; those of a side connected by a thin-walled, whitish seminal groove ; each groove slightly bent laterally at the male pores, in XVIII. Female pores in the anterior half of XIV, in

front of setae *b*. Spermathecal pores mostly unrecognizable, sometimes surrounded by distinct oval fields, in 7/8 and 8/9, sometimes immediately below setal lines *b*, sometimes in the upper half of *bc*; in 5% of worms (136 clitellate specimens examined) the pores in 7/8 are in the upper half of *bc* and those of 8/9 shortly below *c* lines.

Gizzard strong, clearly distinguished from the oesophagus. Calciferous glands arising laterally from the oesophagus, in IX, rounded, of the ocnodriloid type. Intestine commencing in XII. Last hearts in XI, lateral. Testes, sperm masses and funnels free in X; seminal vesicles in IX and XI, the latter pair displacing 11/12 and sometimes 12/13 posteriorly. Prostates with an irregular course below the gut, ending between XXIII and XXVIII; duct much thinner than the glandular part, of variable length, penetrating only a single septum or extending through 3 segments. 1 pair of ovaries and funnels, in XIII. Spermathecal duct mostly thinner than the broadly oval ampulla and somewhat longer, bent in various ways.

DISTRIBUTION. Brazil: Marajo Island, at Cachoeira do Arari (banks of a river).

REMARKS. Clearly this species is close to *E. saltensis*, as Righi has stated, although the form of the spermathecae and the location of the male pores lateral, rather than median of, the prostatic pores clearly distinguish it from the latter species and the internal structure of the calciferous glands is apparently distinct.

Eukerria weyenberghi Cordero, 1942

Eukerria weyenberghi Cordero, 1942: 279, Fig. 9-11.

l = 37-68 mm, w = 3-4 mm, s = 59-109. Epilobous. Setae: *ab* = *cd*, *aa* = *bc* = 3 *ab*; *dd*:*u* = 0.5. Nephropores in *c* lines. Clitellum annular, XIII, $\frac{1}{2}$ XIII-XX; some or nearly all of the ventral and dorsal couples may be obscured; all intersegmental furrows obscured except 13/14 which is partially visible. Prostatic pores two pairs of widely open elliptical slits level with the general body surface, not on papillae, surrounded simply by an "eyelid" like zone formed solely by modification of the cuticle; the centres of the pores in *b* lines, their internal margins in *a*. Seminal grooves absent. Male pores visible with difficulty on XVIII in line with the external margins of the prostatic pores and midway between the latter. Female pores on XIV near the anterior border, in *b* lines at the bottom of a little marked transverse furrow. Spermathecal pores visible on separation of the borders of the intersegmental furrows 7/8 and 8/9 as minute simple orifices in *b* lines.

Last septal glands in VII, in which the gizzard is present though no thicker than the remainder of the oesophagus. Calciferous glands "grape-seed shaped", arising ventrally from the oesophagus and extending anteriorly; internally with a central cavity with radial septa inserted on its periphery. Last hearts in XI. Testes and funnels free in X; seminal vesicles one pair, in IX. Prostates longer than those of any other known species, extending *in situ* to XXXII, the sinuous glandular region, which is quadrangular in section, occupying a length of 8 mm (its actual length about 3 times this); duct somewhat narrower, circular in section, smooth and muscular and coiled in a spiral, extending into XXII; about one eighth the length of the glandular portion. Prostatic ducts discharging on muscular hemispherical papillae

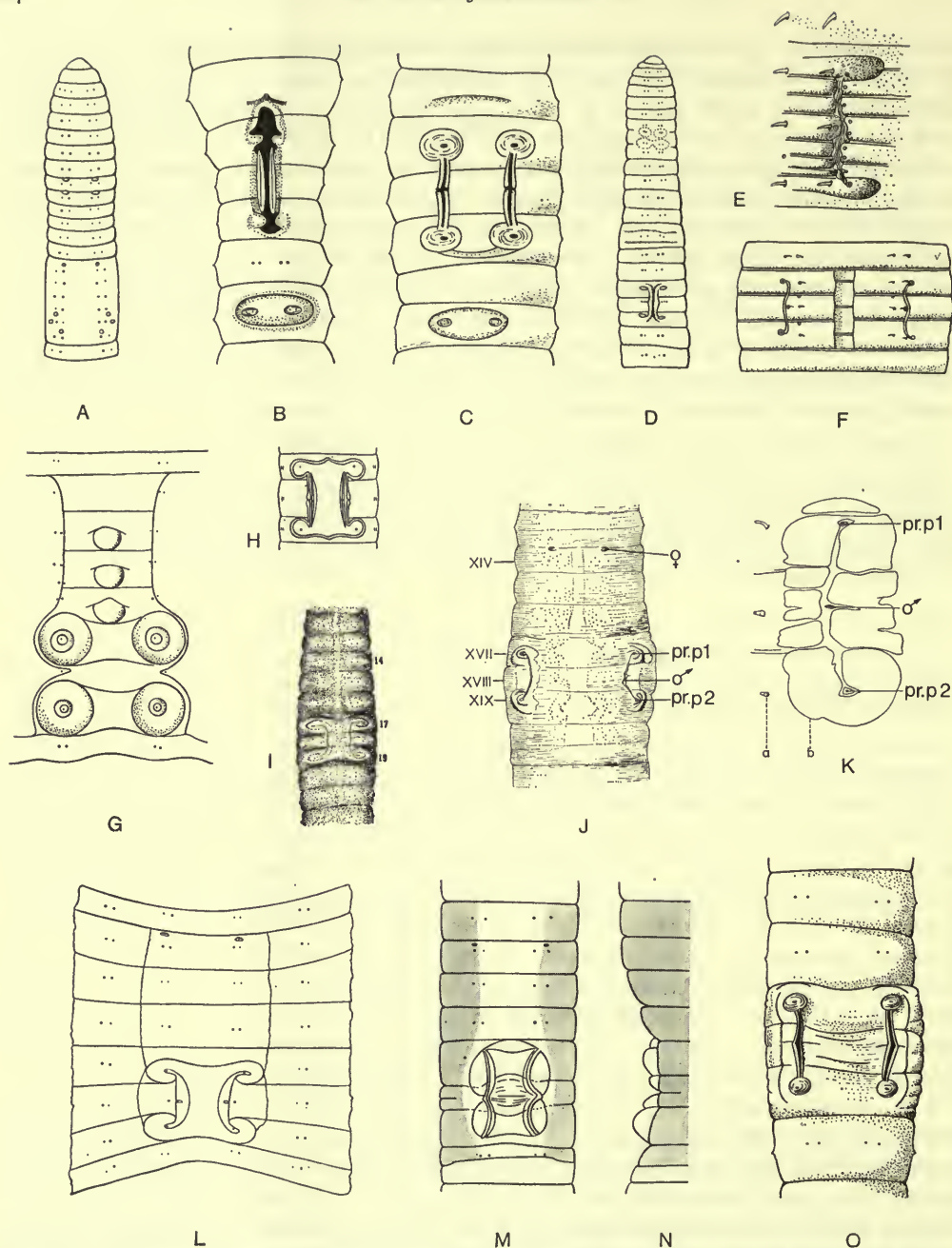


FIG. 9. *Eukerria*, reviewed illustrations of male genital fields. A, *E. halophila* (after Beddard, 1892) ; B-D, *E. kukenhali* : B and C, *E. asilis* (after Righi, 1968) ; D, syntype (after Michaelsen, 1908) ; E and F, *E. mcdonaldii* (after Eisen, 1893) ; G, *E. papillifera* (after Rosa, 1895b) ; H, *E. subandina* (= *Kerria borelli*) (after Cognetti, 1900) ; I, *E. subandina* (after Gavrilov, 1967) ; J, K, *E. saltensis* (after Jamieson, 1967) ; L, *E. subandina* (after Rosa, 1895b) ; M and N, *E. tucumana* (after Cordero, 1942) ; O, *E. urna* (after Righi, 1968).

corresponding with the external pores and containing a large "atrial" chamber. Prostatic duct joining the postero-medial aspect of the internal papilla. Spermathecae 3 mm long by 1 mm wide ; the ampulla large and pyriform ; each flexing around the oesophagus which is in contact with the duct. The duct wide and ampulliform, distinguishable by its texture and greater opacity ; equalling the ampulla in length.

DISTRIBUTION. Argentina : Buenos Aires Province, Islas del Tigre (Habitat?).

REMARKS. It seems probable that the internal papillae (bursae?) at the ends of the prostatic ducts are capable of eversion or protrusion to give external papillae of the type seen in other species of *Eukerria*.

DISCUSSION

Within the tribe Ocnerodrilini (= Ocnerodrilinae s. Gates, 1966), only *Eukerria*, *Kerriona* Michaelsen, 1924, and *Maheina* Michaelsen, 1899b, display the acanthodrilin condition of the male pores, with the prostatic pores on XVII and XIX and the openings of the vasa deferentia intermediate on XVIII. An especially close relationship between *Maheina* and *Eukerria* can be rejected as the single species of *Maheina* differs from *Eukerria* in its setal ratios (the setae of the fore- and mid-body being widely separated), in location of the gizzard in VI, in possessing two pairs of calciferous glands ; in having testes in X and XI, and geographically, being the only Ocnerodriline known from the Seychelles.

A close relationship between *Eukerria* and the two known species of the Brazilian genus *Kerriona* was proposed by Stephenson (1930) as *Kerriona* besides having acanthodrilin male terminalia has the testes confined to segment X as in *Eukerria*, such proandry being known elsewhere in the Ocnerodrilinae (s. lat) only in *Haplo-drilus* Eisen, 1900 and, now, in *Gatesia* Jamieson, 1962. Contrary to the views of Michaelsen (1924) and Stephenson (1930), the terrestrial mode of life of *Kerriona* cannot be considered a valid distinction from *Eukerria* as some species of the latter genus are known only from terrestrial habitats. Nevertheless, *Kerriona* shows morphological distinctions which set it apart from *Eukerria* and which suggest that the mutual possession of proandry and acanthodrilin male terminalia in the two genera does not indicate a closer relationship between the two genera than either has with other genera of the Ocnerodrilini. Of the few known characteristics of *Kerriona*, those which indicate that it is phyletically and phenetically distinct from *Eukerria* are wide pairing of setae in at least the mid and hindbody ; the panicked-tubular or tubular calciferous glands, and the presence of an intestinal typhlosole.

In the subfamily Octochaetinae variation from the acanthodrilin condition to the microscolecin condition (a single pair of male and prostatic pores, on XVII) of many ocnerodriles occurs within a single genus, *Lennogaster*, and therefore the possibility of close relationship of *Eukerria* and non-acanthodrilin ocnerodriles deserves attention. At present there is, however, no convincing evidence for such a relationship though Gates (1957), in a key to the genera of the Ocnerodrilinae, placed those species of *Eukerria* which lack gizzards in an *Ocnerodrilus*-group of species. He stated that *Eukerria* must be restricted to those species with a gizzard in segment VII

and went so far as to specify that "*Kerriona* may be closer to *Ocnerodrilus* than to its supposed ancestor *Kerria*".

With regard to relationships within *Eukerria* there can be no *a priori* justification for segregation of species which lack a gizzard from the remainder of a genus in which development of the gizzard varies from weak to strong, as Jamieson (1963) showed for the genus *Nannodrilus*, but perusal of the accounts given above in the systematics section does reveal that absence of gizzards correlates with other distinctions in one group of species. Some grounds therefore exist for recognizing subgroups within *Eukerria* though elevation of these to generic rank seems inadvisable in view of the many gaps in our knowledge of the genus.

This agiceriate species-group is the only clearly defined subgroup which the author is able to recognize from the present limited evidence. It may be termed the *stagnalis*-group and contains only *E. stagnalis*, *E. papillifera* and *E. weyenberghi*. These species share a number of characters which are individually or at least in combination very distinctive. They are :

- (i) absence of a gizzard, at least as a recognizable swelling of the oesophagus (only in *E. rubra*, elsewhere in the genus, is a gizzard said to be absent) ;
- (ii) location of the prostatic pores in line with the ventral setal couples (a condition occurring elsewhere in *E. halophila*, *E. kukenthali*, *E. tucumana* and *E. urna*) ;
- (iii) presence on the prostatic ducts of ectal bursae, which do not occur elsewhere in the genus ;
- (iv) the absence (*E. papillifera* and *E. weyenberghi*) or slight development (*E. stagnalis*) of seminal grooves (doubtfully absent in *E. halophila* and *E. rubra*) ;
- (v) extension of the prostatic glands through many segments, a feature seen also in *E. kukenthali*.

The structure of the calciferous glands is not known for *papillifera* but in *weyenberghi* small parietal septa were seen by Cordero (1942), a condition which does not conflict with that in *E. stagnalis* (p. 154) in which, however, some septa are known to fuse centrally. Cordero's statement that in *weyenberghi* a gizzard is present in VII, though no wider than the oesophagus, would, if correct, suggest real affinity of the *stagnalis* group with other species of *Eukerria*. The extensive series of precardiac commissural vessels in *E. stagnalis* appears to be a primitive feature but, from the evidence of *weyenberghi*, it appears more likely that absence of the gizzard in *stagnalis* and *papillifera* is secondary. Subgeneric or even separate generic status for the *stagnalis* group is not without justification but the apparently close relationship with *Eukerria* and the paucity of our knowledge of the latter do not warrant making such distinctions at present.

In the absence of taxonomically important information with regard to several systems in many species of *Eukerria*, the character which appears most likely to permit subdivision of the remaining *Eukerrias* into morphologically and, presumably, phylogenetically distinct groups is the internal structure of the calciferous glands. Three categories may be distinguished on the basis of this character as shown below.

STRUCTURE OF THE CALCIFEROUS GLANDS IN *EUKERRIA*

* personal examination

(I) Walls very thick and not projecting as septa or as folds into the lumen (Fig. 10E)

*E. limosa**E. pascuorum**E. subandina** and its junior synonym *E. borelli***E. rubra*?

(II) Transitional. Walls very thick but with a few longitudinal folds though with no defined complete or incomplete septa (Fig. 10D)

*E. rosae**E. saltensis**

(III) Walls relatively thin. Parietal septa well defined and numerous (Fig. 10A-C)

*E. eiseniana** and its junior synonym *E. hortensis**E. garmani***E. halophila*?*E. kukenthali**E. tucumana**E. urna**E. mcdonaldi*? (or II)and the *stagnalis*-group species, *E. stagnalis**, *E. weyenberghi*.

Internal structure unknown.

E. asuncionis and *E. papillifera*.

Information on several of the species listed is inadequate and the extent of individual variation needs to be investigated but this albeit crude classification serves to suggest a starting point for further subdivision of the genus.

After removal of the *stagnalis*-group it is not possible to place all the remaining species in subgroups though some groupings are observable. In group I, *E. limosa* and *E. pascuorum* are morphologically similar or perhaps synonymous. The two species of group II, *E. saltensis* and *E. rosae* appear to be closely related though distinct species. Of the group III species, few affinities are discernible, again largely because of lack of data. *E. eiseniana* and *E. garmani* are mutually close but the glands of *eiseniana* are larger and have more delicate and more numerous septa than those of *garmani*. *E. mcdonaldi* isolated in Baja California, stands apart in possessing a type of spermathecal diverticulum. Affinities of the other species, *E. tucumana*, *E. urna* and the type-species, *E. halophila* with other species are uncertain though they must at least for the time being be regarded as congeneric. *E. urna* resembles *E. saltensis* more than it does other species but its ocnodriloid calciferous glands are a noteworthy difference. *E. tucumana* appears to have its closest affinities with *E. garmani*.

It is hoped that drawing together our limited knowledge of *Eukerria* in this account will stimulate further investigation of the genus, ideally by workers in South America, and that sufficient data will be forthcoming to permit a taxonomic investigation of the affinities of its species.

The species of *Eukerria* recognized as valid in the present work, their junior

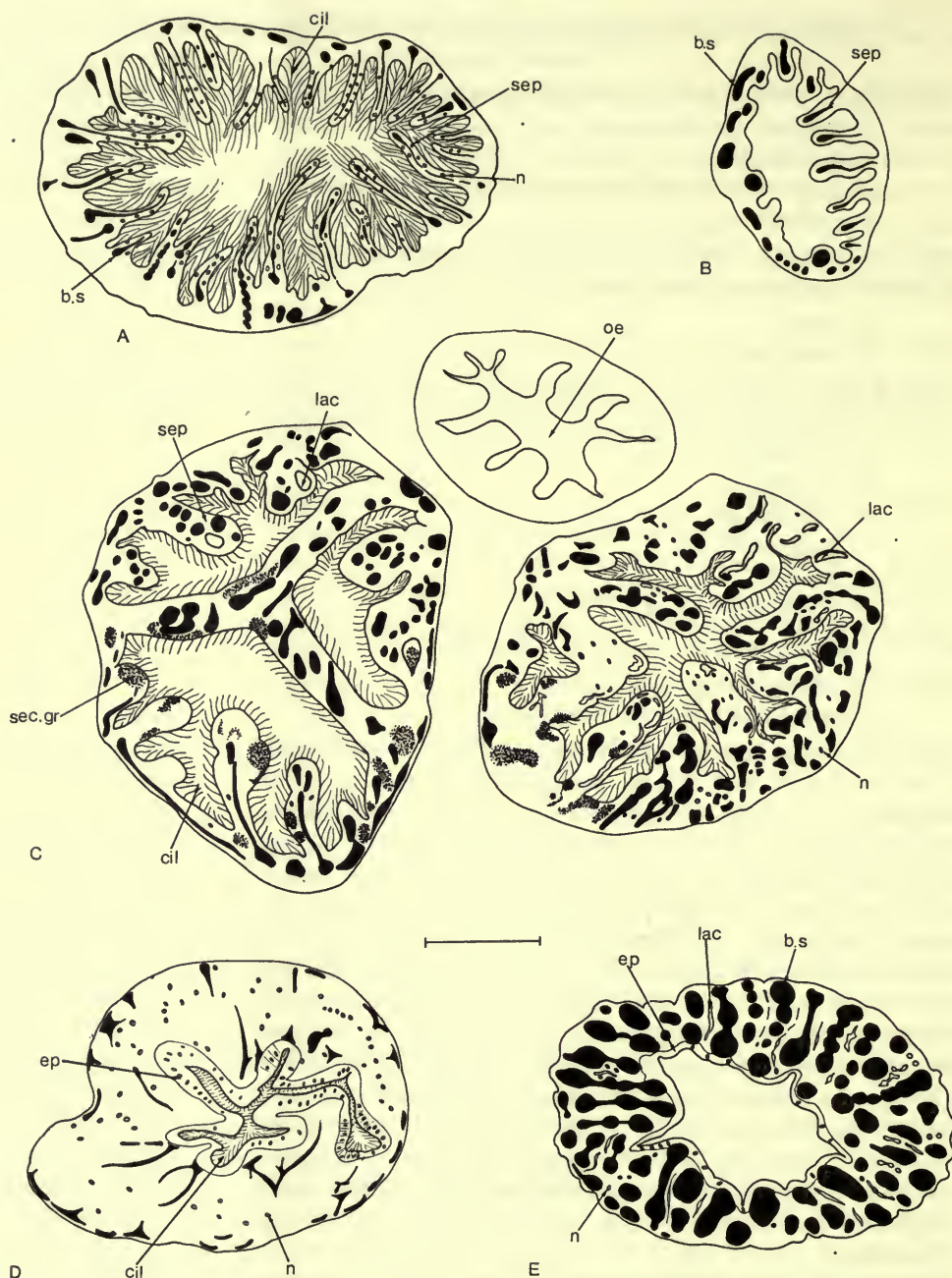


FIG. 10. Calciferous glands in transverse section. A, *Eukerria eiseniana*, syntype, Torino Museum, ol. 110, ex. 295; B, *E. garmani* (*garmani*), syntype, Torino Museum, ol. 111; C, *E. stagnalis*, syntype (small morph) of *E. spegazzini*, Torino Museum, ol. 114, ex. 191, showing two glands and the oesophagus; D, *E. saltensis*, specimen from the Great Berg River, South Africa, author's collections; E, *E. subandina*, syntype of *E. borelli*, Torino Museum, ol. 106, ex. 497. (All to the same scale).

synonyms, their distribution, and the sources of material examined are set out in the taxonomic summary below.

TAXONOMIC SUMMARY

Species here recognized	Junior Synonyms + = new synonymy	Museum material examined B.M. = British Museum T. = Torino Museum H. = Hamburg Museum * = Type material	Distribution
1. <i>E. asuncionis</i> (Rosa, 1895)		T*	Paraguay
2. <i>E. eiseniana</i> (Rosa, 1895)		T*	Paraguay
	<i>K. hortensis</i> Stephenson, 1931 ⁺	B.M.*	Paraguay
3. <i>E. garmani</i> (Rosa, 1895)		B.M. T*	Paraguay; Argentina
4. <i>E. halophila</i> (Beddard, 1892)		—	Bolivia (?) : upper reaches of the Pilcomayo
5. <i>E. kukenthalii</i> (Michaelsen, 1908)		B.M. H*	St. Thomas, West Indies; Christmas Island, Indian Ocean
	<i>K. selangorensis</i> Stephenson, 1931	B.M.*	Selangor, Malaya
	<i>E. peguana</i> Gates, 1942 ⁺	—	Burma
	<i>E. asilis</i> Righi, 1968 ⁺		Brazil : Marajo Island
6. <i>E. limosa</i> (Stephenson, 1931)		B.M.*	Paraguay
7. <i>E. mcdonaldii</i> (Eisen, 1893)		—	Baja California
	<i>K. zonalis</i> Eisen, 1893 ⁺	—	Baja California
8. <i>E. papillifera</i> (Rosa, 1895)		T*	Paraguay
9. <i>E. pascuorum</i> (Stephenson, 1931)		B.M.*	Paraguay
10. <i>E. rosae</i> (Beddard, 1895)		B.M.* T* H*	Argentina
11. <i>E. rubra</i> (Friend, 1916)		—	Oxford botanical gardens
12. <i>E. saltensis</i> (Beddard, 1895)		B.M.*	Chile-mainland and Juan Fernandez Is ; Argen- tina ; Burma ; S. Africa ; Queensland
	<i>Acanthodrilus sydneyensis</i> Sweet, 1900	—	New South Wales ; Vic?
	<i>K. gunningi</i> Michaelsen, 1913	H*	South Africa ; New Cale- donia
	<i>K. nicholli</i> Jackson, 1931	—	South West Australia

TAXONOMIC SUMMARY (*continued*)

13. <i>E. stagnalis</i> (Kinberg, 1867)	—	Uruguay
<i>Acanthodrilus spegazzini</i> Rosa, 1890	T* H.	Argentina ; Brazil
14. <i>E. subandina</i> (Rosa, 1895)	T*	Argentina
<i>K. borelli</i> Cognetti, 1900	T* H*	Brazil
15. <i>E. tucumana</i> Cordero, 1942	—	Argentina
16. <i>E. urna</i> Righi, 1968	—	Brazil : Marajo Island
17. <i>E. weyenberghi</i> Cordero, 1942	—	Argentina

ACKNOWLEDGEMENTS

This study was made possible through the kind cooperation of Mr. R. W. Sims, British Museum (Natural History), Dr. M. Dzwillo, Zoologisches Museum, Hamburg, and Dr. L. Parenti of the Museo ed Istituto di Zoologia Systematica, University of Torino to whom the author gratefully extends his thanks. Serial sections were prepared by Mr. J. Casey. The work was financed by the Canadian National Research Council and University of Queensland Research Grants. Special thanks are due to Professor R. O. Brinkhurst for facilities provided.

ILLUSTRATIONS

With the exception of Fig. 9, the illustrations have been drawn by the author by camera lucida. The scale indicated is 1 mm unless otherwise labelled. Shaded areas represent the clitellum.

Abbreviations used in the illustrations :

b.s, blood sinus ; c, cerebral ganglia ; ca. g, calciferous gland ; cil, cilia ; d.v, dorsal blood vessel ; dv. h, dorsoventral (lateral) heart ; ep, epithelium ; ♀, female pore ; gi, gizzard ; g.m, accessory genital marking ; g.m.b, bursa corresponding with external genital marking ; int. v, intestinal (oesophageal) valve ; lac, cavity or lacuna ; lo, latero-oesophageal vessel lo.h, latero-oesophageal hearts ; ♂ male pore ; ♂ f, seminal funnel ; n, nucleus ; n.c, ventral nerve cord ; np, nephropore ; oe, oesophagus ; ph, pharynx ; pr. d, prostate duct ; pr. g, glandular part of prostate ; pr. b, prostatic bursa ; pr. p, prostate pore ; pr. po, prostate porophore ; pro, prostomium ; sec. gr, secretory granules ; sem. gr, seminal groove ; sep, septum ; sep. g, septal gland ; sp, spermatheca ; sp. p, spermathecal pore ; s.v, seminal vesicle ; t, testis ; v.d, vas deferens ; v.d.b, ectal thickening (bursa) of vas deferens.

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BARRIE G. M. JAMIESON, Ph.D.
Zoology Department
UNIVERSITY OF QUEENSLAND
ST. LUCIA
BRISBANE
QUEENSLAND, AUSTRALIA

Printed in Great Britain by
Alden & Mowbray Ltd
at the Alden Press, Oxford

OBSERVATIONS ON THE ELECTRA
DOLPHIN, *PEPONOCEPHALA*
ELECTRA



W. A. DAWBIN, B. A. NOBLE, F. C. FRASER

BULLETIN OF
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ZOOLOGY

Vol. 20 No. 6

LONDON : 1970

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BY

WILLIAM HENRY DAWBIN

BRUCE ALEXANDER NOBLE *Xref.*

FRANCIS CHARLES FRASER

Pp. 173-201 ; 13 Text-figures

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By W. H. DAWBIN, B. A. NOBLE & F. C. FRASER

INTRODUCTION

THE notes set down in this paper were stimulated by a stranding of electra dolphins at Crowdy Heads, about 200 miles north of Sydney in August 1958. This stranding was reported briefly as a school of blackfish by a local newspaper some days after the event. Following notice of the report one of the authors (W.H.D.) made local enquiry and was told that all the animals had been removed by fishermen and had been cut up for bait. The local postmistress, Mrs. W. J. Ward, had made a careful count of the teeth of one specimen before its removal and stated that there were 22 on each side of the upper jaw and 19 on each side of the lower jaw. This eliminated the possibility that the school might have been pilot whales (*Globicephala* sp.) the species usually referred to locally as blackfish. The observed tooth row number also ruled out *Feresa* from consideration.

An immediate search in the Crowdy Heads area failed to unearth any skeletal remains, so with the co-operation of the Australian Broadcasting Commission, both radio and television, appeals were made for any photographs or material which may have been taken by visitors to the beach on the day of the stranding. The response in colour and black and white photographs and in descriptions was good, and a number of the photographs showed quite clearly that most of the animals had a rounded snout without beak, white lips and light thoracic and abdominal patches on an otherwise uniformly dark-coloured background.

During a further visit to the Crowdy Heads area 1962 (by W.H.D.) reports inland from the area where received that in the course of removal of the dolphin carcasses one had fallen off a truck and had been left behind at the roadside. The skull had been removed by a local resident, Mr. H. Anderson, who generously presented it to the visiting author.

Subsequently a half skull which had been used as bait in a fish trap was secured. This specimen was from a dolphin that had stranded in the Port Macquarie area in January 1962. The unprompted description of the dolphin by the fisherman concerned matched those at Crowdy Heads. He had seen the latter animals and was convinced that his specimen was identical with them.

The number of alveoli in the skull of the decomposed carcase and in the half skull essentially confirmed Mrs. Ward's tooth count and from this and from other skull characters the school was provisionally identified as *Lagenorhynchus* (= *Peponoccephala*) *electra* (by W.H.D.). The two specimens were sent to the British Museum (Natural History) for comparison with other examples of this species including the holotype.

OBSERVATIONS ON THE CROWDY HEADS AND
PORT MACQUARIE STRANDINGS (W.H.D.)

Letters referring to the animals prior to stranding were unanimous in describing them as a large school of black dolphins sighted off Port Macquarie heading south between 2 and 4 p.m. on the day preceding the stranding. Crowdy Heads is approximately 40 miles south of Port Macquarie and the animals reached there and commenced stranding during a high tide about 10 a.m. the following morning, along a gently shelving stretch of sandy beach. They stranded in more or less a line with heads facing away from the sea and the animals were spread between a quarter and half a mile of beach. Number estimates range from 150 to 250 in the school and none was seen which did not come ashore. A few which were pushed out to sea returned fairly quickly and became stranded again. Length estimates state that the school contained small young about 3 ft in length but were mostly about 8 ft with some possibly up to 10 ft ; however actual measurements do not appear to have been made. A considerable proportion (some writers state up to 50% :) were pregnant females and there was agreement that the foetuses were of similar size estimated as 2'6" to 3'0" and judged by appearance as near full term. A photograph of one foetus held up by a fisherman is consistent with the size estimate. The observations on foetuses and also of apparently new born young suggest a relatively circumscribed breeding period during spring.

No observations on stomach contents were reported but there were several reports of small thread-like worms " as a crawling mass in the heads. " These appear to have been common and resemble the report of Nakajima and Nishiwaki (1965) on the presence of many nematodes in the air sinuses of the skull.

The occurrence of these animals in a single school of 150-250 and the report of another and larger school off Japan in 1965 (Nishiwaki and Norris, 1966) indicate that this is a schooling species, despite the isolated nature of each of the skulls received. A smaller group (estimated as about two dozen) has been reported by a fisherman (Mr. L. Elford) who collected specimens from the Crowdy Heads school and also obtained the Port Macquarie specimen. These were stranded at Diamond Head, a few miles from Port Macquarie and all were cut up and completely used for bait. Other local fishermen recognised that the size, colour pattern and head shape differed from the usual local dolphins and agreed with those at Crowdy Heads. They also report occasional sightings of similar schools at about the edge of the continental shelf along the neighbouring coast. It is therefore possible that *P. electra* is not particularly rare along the coast of northern New South Wales but that it is a species which normally remains some distance from land.

External features

The earliest representation of the external appearance of the electra dolphin is provided by Peale (1848) and is reproduced in True (1889).

The lateral view of the animal shows it to be darkly pigmented over most of the body, but showing a white patch midway between lower jaw and flipper and an elongated white ventral area extending from some way in front of the level of the

anterior margin of the dorsal fin, to a level midway between dorsal fin and tail. There is indication of a white lower lip and lighter pigment around the eye.

The next figure of external appearance is that of Owen (1866), (his plates 5, fig. 1 and 7, figs. 1-5) with reference to *L. fusiformis* (a synonym). This reference is given only to emphasise the error in representation of the electra dolphin.

Goodwin (1945) reproduced the drawing made by Robert Cushman Murphy of an electra dolphin taken in the tropical Atlantic in 1912. This drawing shows an absence of pigmentation around the mouth and on the throat, but no white area more posteriorly on the belly. A noteworthy feature is a ventrally projecting, long, low eminence in the post-anal region.

The photographs included in Nishiwaki and Norris (1965) best show the external form and pigmentation. These authors give a description of shape, particularly of the head, in connection with the erection of the genus *Peponocephala* to include *P. electra*, because of the absence of a well defined rostrum. The various pictures show the electra to be predominantly darkly pigmented. The white mouth area is conspicuous and in the ventral view the broad, unpigmented throat area behind the deeply pigmented lower jaw area, links up with the white patch seen in lateral view in Peale's and Goodwin's figures. At about the level of the flipper, the dark pigmentation extends from the side down to the mid ventral line. Behind this, a lenticular unpigmented area, extends from umbilicus to anus ; this area again is the same area seen in restricted lateral view in Peale's figure.

Specimens

The following specimens were available for survey :—

No.	Reg. No.	Comments
1	B.M. (N.H.) 1844.10.5.3	Type of <i>Lagenorhynchus electra</i> Gray, 1846 Zool. Erebus & Terror, I (Mammalia) 35, pl. 13. [ADULT in growth comparison]
2	B.M. (N.H.) 1866.2.5.1 1475a	Type of <i>Delphinus fusiformis</i> . Owen, 1866 Trans. Zool. Soc. London, 6 : 22, pl. 5, fig. 1, pl. 7, figs. 1-5.
3	B.M. (N.H.) 358a	Type of <i>L. asia</i> Gray, 1846 Zool. Erebus & Terror I (Mammalia) 35, pl. 14.
4	W.A.M. 4798	Salt marsh at Derby ; W. Australia. Skull and skeleton.
5	A.M.N.H. 4300	♂ found at 3°03'N 24°40'N in Atlantic. Goodwin 1945 J. Mammal 26 : 195.
6	B.M. (N.H.) 1959.7.9.2.	♂ Hittadu Is., Addu Atoll. Gan Maldives. Skull and skeleton. [ADOLESCENT in growth comparison]
7	—	New South Wales. No lower jaw. [JUVENILE in growth comparison]
8	—	New South Wales. Half skull, no lower jaw.
9	B.M. (N.H.) 1965.6.2.1	♂ Kahuku, Oahu, Hawaii [NEWBORN in growth comparison]
10	—	♂ Hiratsuku. Nakajima & Nishiwaki 1965. Sci. Rept. Whales Res. Inst. 19 : 91-104. (Readings taken from paper)

Osteological features

The type of *Lagenorhynchus electra* Gray (Reg. No. 1844.10.5.3) is represented by a skull and lower jaw. The pointed conditions of the teeth indicate that the skull is of a mature but not aged specimen.

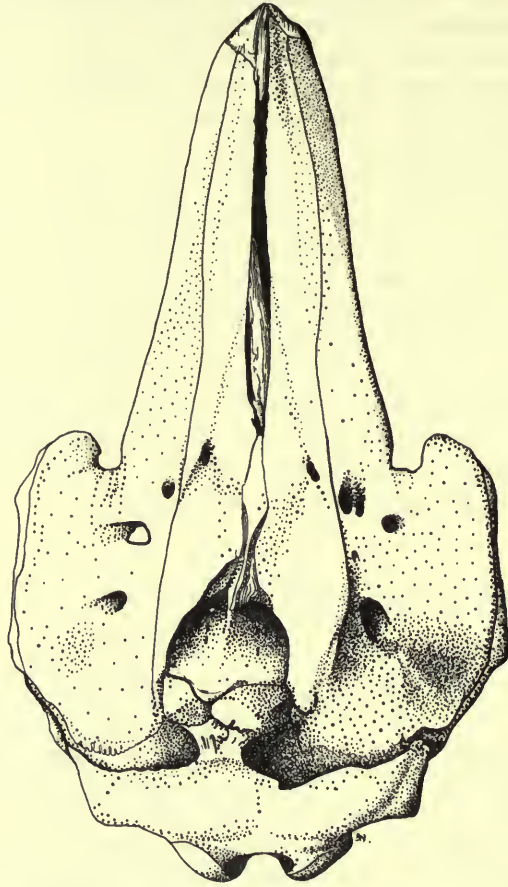


FIG. 1. *Peponocephala electra* 1844.10.5.3. type. Dorsal view, Orthographic projection.

In lateral view, the type skull is wedge-shaped, with the occipital condyle extending prominently from the base. The supraoccipital sweeps up to form the supraoccipital crest, which is connected to a prominent boss formed by the nasals, by a distinctive isthmus. The rostrum extends forwards from the cranium to form the apex of the wedge.

Rostrum. The rostrum is represented by the forward extension of the maxillae, premaxillae, vomer and mesethmoid cartilage beyond a line drawn between the caudal margin of the antorbital notches. In outline, dorsally (fig. 1) starting from the antorbital notches, the rostrum is shallowly concave, almost immediately becoming extendedly convex; it again becomes shallowly concave to about the mid-rostral

length, where a convexity is initiated, which increases distally as the two maxillae approximate to each other. The proximal convexity is associated with a crest which is most obvious when viewed from the side.

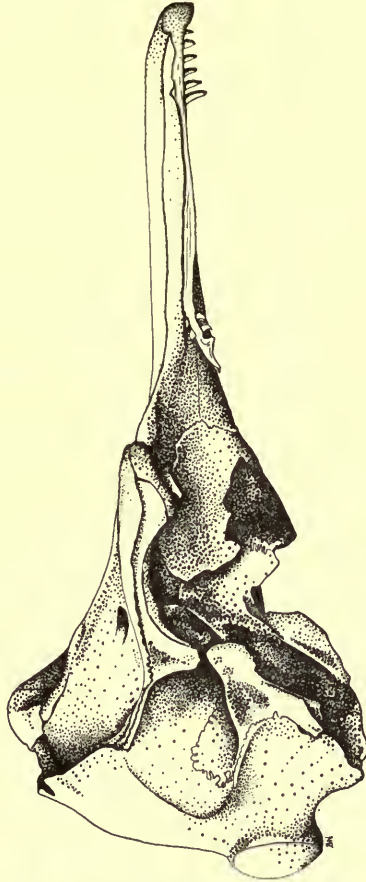


FIG. 2. *P. electra* 1844.10.5.3. type. Lateral view. Orthographic projection.

Proximally the dorsal surface of the rostrum is flattened transversely, with its lateral maxillary margins slightly upturned (fig. 2). Further forward the rostrum becomes more convex, its regular contour being interrupted by a flexing of the medial borders of the premaxillae into a pair of crests so that with the cartilaginous extension of the nasal septum between them, they form a blunt keel.¹

When the skull is viewed ventrally (fig. 3) it is seen that the distal portions of the rostrum are covered with dried palatine tissue, hiding the osteological features. Most of the ventral bony tissue is maxillary, but in the mid line, judging from other *P. electra* skulls, a sliver of vomer may be seen, with premaxillae exposed anteriorly to it.

¹ There is a gap between the two premaxillae dorsally, extending the length of the rostrum, filled with a cartilaginous extension of the nasal septum.

The tooth rows are short compared with the length of the snout ; and they are ventrally directed. The alveoli are discrete.

There are sutures between palatines and maxillae, though laterally the palatines are squamous over the maxillae.

The pterygoid hamuli are damaged, the bone of the ventral region missing, exposing the sinuses of the pterygoid hamuli.

Cranial Region. This is represented by the portion of the skull that lies behind the line joining the caudal margins of the antorbital notches.

When viewed dorsally (fig. 1), the cranial region of the skull is dominated by the large maxillary plates, whose margins show the deep indentations rostrally of the antorbital notches, and laterally they form the supraorbital margins. These supraorbital margins are nearly parallel with slight protrusions of the supraorbital processes of the frontals from under the maxillary plates, to form the pre- and postorbital processes. The margin runs obliquely backwards from the postorbital process until the line flows into the general shape of the cranium proper.

The essential rounded shape of the cranium is interrupted by the elevation formed by the posterior borders of the post-temporal fossae.

The cranium is traversed coronally by the supraoccipital crest, which forms a shallow anteriorly concave arc.

The maxillary plates which present by far the greatest area dorsally are spread widely over the frontals so that the latter are visible laterally only to the most limited extent. In their rostral portions the maxillary plates are roughly horizontal but curve upwards posteriorly toward the vertex of the skull, being separated there by the nasals. The maxillae extend to meet the base of the supraoccipital crest laterally, but medially in the area between the crest and maxillae, the frontals are exposed. There are conspicuous foramina in the maxillary plates, five on the right and three on the left.

The external nares are bounded caudally by the ossified mesethmoid, laterally for most of their extent by the internal margin of the premaxillae, but rostrally by the maxillae which have emerged on the dorsal surface of the skull. Cartilaginous elements between the maxillae and nasal septum are problematical in origin. The nasal region as a whole best illustrates the asymmetry of the skull.

The left premaxilla does not extend posteriorly to the nasal bone, whereas the right premaxilla extends half way along the right nasal bone.

The left premaxilla is altogether narrower than the right, to about the level of the premaxillary foramen.

The isthmus (formed by interparietal) of the nasal boss is situated to the left of the midline.

The left nasal is smaller than the right, the latter extending to the left of the midline of the skull.

Ventrally (fig. 3), the skull is divided by the two basicranial crests, with the basicranial trough running between them from the opening of the internal nares to the occipital condyles. To the side of the crest may be seen the supraorbital process of the frontal, with jugal (with the stump of the broken jugal arch) and sphenoids visible, together with their various associated foramina. Posterolaterally, the robust

zygomatic process of the squamosal extends anteriorly toward the postorbital process, and with it forms an arch through which the temporal muscles pass. The external surface of the zygomatic process is rugose, with a definite depression within its margin ; the dorsal surface is smooth ; the ventral aspect is divided into articular and sinus areas.

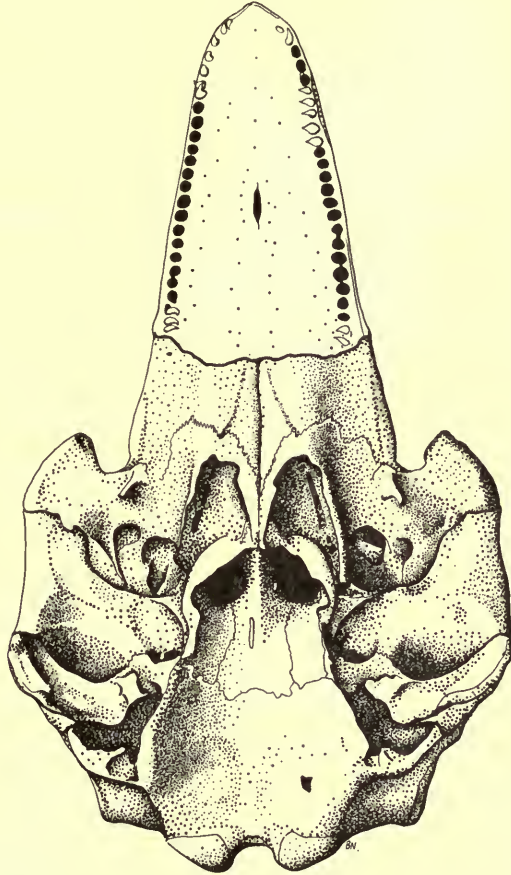


FIG. 3. *P. electra* 1844.10.5.3. type. Ventral view. Orthographic projection.

The bones of the ventral surface (figs. 3 & 4) of the skull give an indication of the extent of the air sinuses. On either side the pterygoid sinus extends medially as a pronounced excavation below the pterygoid portion of the basicranial crest ; the sinus extends into and fills the pterygoid hamulus. The middle sinus is situated on the ventral aspect of the zygomatic process and is extensive in area. The posterior sinus excavates the paroccipital process slightly. The orbital sinus is bilobed and this division is well demarcated by a distinct ridge on the supraorbital process of the frontal ; this evidence suggests that they approximate closer than do the two lobes of *L. albirostris* and *L. obscurus* respectively (Fraser & Purves 1960). The anterior lobe extends a little way anterior to the roots of the jugal arches.

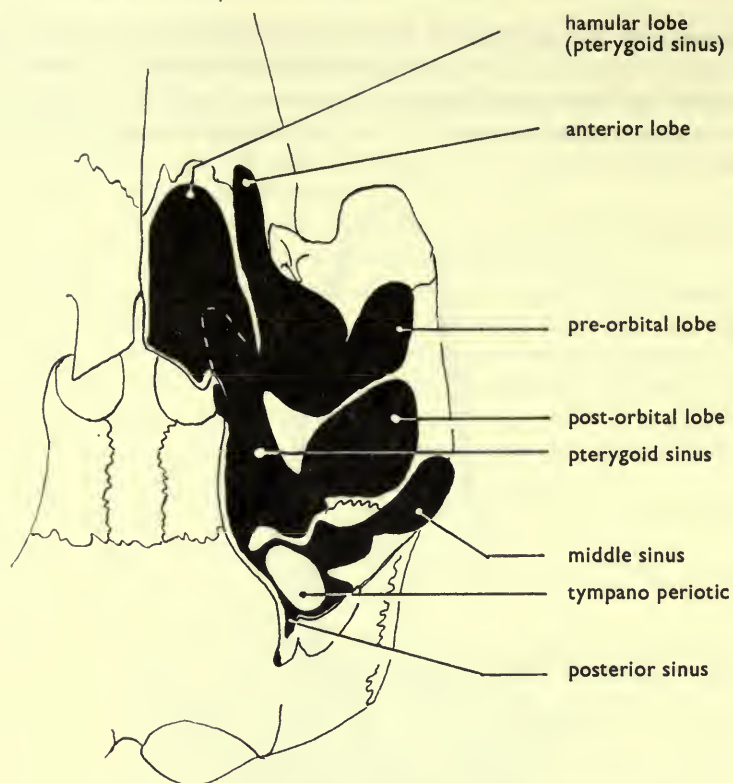


FIG. 4. *P. electra*. Sinus system. Semi-diagrammatic.

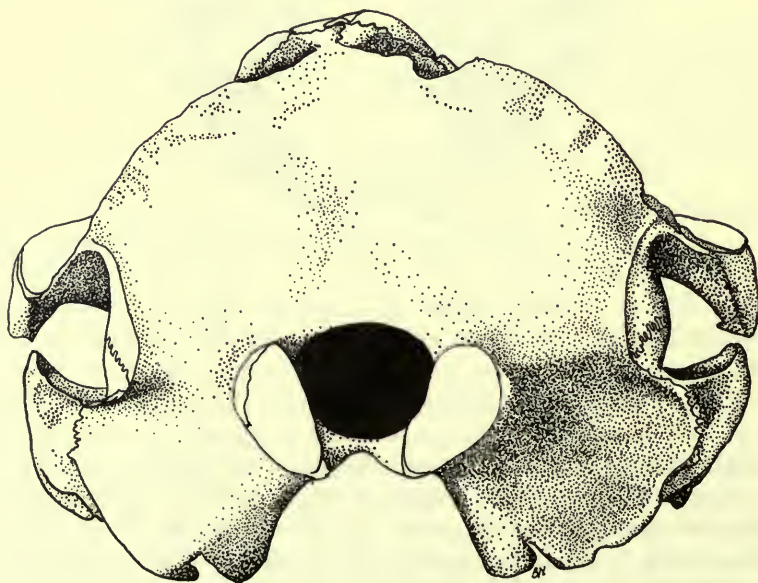


FIG. 5. *P. electra* 1844.10.5.3. type. Caudal view. Orthographic projection.

The post-temporal fossa (fig. 2) is bounded anteriorly by the postorbital process which is contained as a ridge of the exoccipital ; posteriorly the fossa is bounded by a ridge between parietal and exoccipital.

TABLE 2

	% of parietal width									
	1	2	3	4	5	6	7	^{x18}	9	8
1. Condyllo-basal length.	260.6	254.3	246.7	237.5	253.1	229.3	220.3	225.5	195.7	
2. Rostrum length.	140.0	139.4	133.3	127.2	137.6	121.5	112.6	116.3	90.8	
3. " basal width.	79.4	74.3	72.5	67.4	73.7	56.9	54.2	74.5	43.3	
4. " width 60 mm. anterior to ant. ob. notches.	66.3	61.2	57.9	58.7	67.0	48.1	43.4	55.1	30.5	
5. " " at middle.	53.1	52.6	46.2	47.8	52.5	40.9	41.1	43.9	29.1	
6. Premaxillae width at same point	34.8	30.9	31.6	29.7	36.1	25.4	23.2	27.5	14.9	
7. Tip of snout to blowhole.	181.8	177.2	170.8	166.3	177.8	155.2	141.0	—	116.3	
8. " " " pterygoid.	—	169.1	160.8	157.0	162.4	147.0	139.9	—	114.9	
9. Preorbital width.	141.8	134.9	129.8	128.2	129.9	114.9	109.5	120.4	85.1	
10. Post-orbital "	148.0	142.3	140.4	138.0	140.2	121.0	119.1	127.6	95.0	
11. Orbital "	142.3	135.4	128.6	135.8	129.9	113.6	106.5	120.4	87.9	
12. Blowhole, width at	35.4	32.0	36.2	33.8	32.9	28.2	28.6	—	29.1	
13. Zygomatic breadth.	145.7	140.1	136.9	136.8	140.2	121.0	117.9	—	91.5	
14. Greatest width pmx.	54.9	51.4	53.2	50.5	52.1	44.7	48.8	—	41.1	
15. Width of braincase across parietals	100	100	100	100	100	100	100	100	100	
16. Number of teeth upper R.										
17. " " " " L.										
18. Length of tooth row upper R.	104.0	94.9	87.7	—	97.9	—	—	—	59.6	
19. " " " " " L.	104.0	94.9	89.5	—	97.4	—	—	—	60.3	
20. Hinder end of upper tooth row R.	107.4	—	98.2	—	104.1	90.6	—	—	64.5	
21. to tip of pmx. L.	106.9	—	100	—	103.1	91.7	82.7	82.1	65.2	
22. Number of teeth lower R.										
23. " " " " L.										
24. Length of lower tooth row R.	92.0	—	91.8	84.3	85.6	85.1	—	—	66.7	
25. " " " " " L.	94.3	—	89.5	82.1	87.6	85.6	—	—	66.7	
26. Hinder end of lower tooth row R.	95.4	—	94.1	86.4	87.1	87.3	—	—	68.8	
27. to tip of mandible L.	95.4	—	93.0	84.8	90.2	88.4	—	—	69.5	
28. Mandible length.	213.1	206.8	201.8	189.7	201.0	180.0	—	—	146.9	
29. Coronoid height.	48.6	48.6	47.4	36.7	44.8	43.6	—	—	34.7	
30. Length of symphysis.	21.1	20.6	22.8	20.1	19.6	20.4	—	—	14.9	
31. Post-temporal length.	47.4	49.1	46.2	50.5	47.9	45.8	42.3	39.8	38.3	
32. " " height.	32.0	35.4	33.3	35.9	27.8	29.8	27.4	33.2	22.7	
33. $\frac{1}{2}$ rostrum length—width at	40.0	42.9	33.9	38.0	—	29.0	—	—	21.3	
34. Cranial height.	74.3	74.9	73.1	69.6	—	69.6	70.2	68.4	64.4	
35. " length internal.	84.6	76.6	80.4	74.7	—	75.1	75.0	68.9	80.8	

Skull dimensions of *P. electra* and their proportions as percentages of parietal width.

The numbers at the head of the column refer to the list of specimens on page 177.

^{x1} Percentages are to estimated measurement of width of brain case.

The caudal aspect of the skull (fig. 5) is dominated by the great extent of the fused occipital bones. The general contour is interrupted by the occipital condyles with the oval foramen magnum between. The general outline is circular, but is interrupted by the basioccipital crests, paroccipital crests and notches, nasal boss, zygomatic processes and the posterior margins of the post temporal fossae.

Lower Jaw. The lower jaw (fig. 6) is robust, the long axes of the rami making an acute angle with each other where they join at the symphysis, which is short. (The two rami are fused together in this specimen).

The upper and lower margins of the rami are almost parallel up to the hinder end of the tooth row, where they diverge, the upper margin being produced into a low crest between the hindmost tooth and coronoid process. From the coronoid process the margin extends obliquely and rather irregularly to the condyle.

Slightly anterior to the level of the mandibular foramina, the profile of the jaw is produced into a keel, which is continued distally into the anterior profile of the jaw.

The symphysis is short and in ventral view the prow of the jaw is evenly rounded to each ramus anterior to the keels.



FIG. 6. *P. electra* 1844.10.5.3. type. Lateral view right mandible. Orthographic projection.

The tooth rows are again short compared with the length of the jaw, the teeth sitting in discrete alveoli. The proximal teeth are upright in attitude, but proceeding distally they assume an increasingly lateral splay. The crowns of the teeth are separated by a distance of approximately the basal diameter of the teeth.

The dimensions of the type skull and of other available specimens are given in Tables 1 & 2.

GROWTH OF THE SKULL

(a) *Quantitative Discussion.* The changes observed with growth are demonstrated quantitatively. The conventional use of condylobasal length as a base for the comparison of other measurements was discarded in favour of parietal width, following an earlier paper by Fraser and Noble (1968).

It is generally accepted that increase in the size of the brain levels off at a comparatively early stage in the animal's life. The similarity of cranial size in the juvenile and adult indicates conformity to this growth pattern.

To determine the rates of growth of the various parts of the skull, values of the various measurements were plotted against their respective parietal widths on a double logarithmic scale. It may be taken that the rates of growth of the various parts, relative to parietal width, satisfy the equation $y = bx^k$. Where x is the parietal width, y the length of the part, b the fractional coefficient (the value of y when $x = 1$), and k the growth coefficient. Calculated values are shown below (Table 3). Values of k over unity indicate an increasing rate of relative growth and those less than unity the converse; i.e. positive and negative heterogony respectively.

The skull of the new-born animal is essentially a brain box with diminutive rostrum, supraorbital and zygomatic processes. The growth of the skull is predominantly of these extensions from the brain box.

TABLE 3

Peponocephala electra

Table of growth coefficients for various parts of the skull

Reading No.	Measurement	Growth coefficient
1	Condyle basal length :	1.85
2	Rostrum : length :	2.35
3	Rostrum : basal width :	2.90
4	Rostrum : width 60 mm. anterior to ant-orbital notches :	3.50
5	Rostrum : width at middle :	3.00
9	Preorbital width :	2.60
10	Postorbital length :	2.40
13	Zygomatic breadth :	2.70
15	Width of braincase across parietals :	1
33	Rostrum : width at $\frac{3}{4}$ length :	3.20
34	Cranial height :	1.45
35	Cranial length internal :	0.725

The increase of the condylobasal length is by the growth of two components, rostral and cranial. It will be seen from Table 3 that the contribution of rostral length (2.35) to total length is much greater than is cranial length (0.725).

In the rostrum itself growth can be regarded as taking place two-dimensionally, and the table indicates that length, although prominently positively heterogonic is at a lower rate than its lateral expansion. The lateral expansion is not uniform for the whole rostrum. Reading No. 4 is an expression of the lateral expansion that takes place in the basal portion of the rostrum, which is at a lower rate than at the middle of the beak. Towards the tip of the snout (Reading 33) the coefficient indicates a relatively high rate. The interaction of these growth rates is expressed in the shape of the adult rostrum.

In the newborn, the preorbital width is considerably less than the postorbital width (5%), and the projections, which develop laterally, are all of less dimension than the parietal width. The reversal of this condition with age is achieved by the faster growth of these parts compared with the expansion of the brain box.

Development of the postorbital and zygomatic processes result in the enlargement of the post-temporal fossa. In the new-born, this aperture, through which the temporal muscle passes, is small and subtriangular ; by the growth of the zygomatic and postorbital processes it becomes rounder and is visible in the caudal aspect of the skull of the adult.

The coefficients showing development of the brain box (reading 15, 34, 35) indicate a lower rate than for any of the other dimensions considered. But the coefficients of growth throughout the animal's life do not take into account the established fact that brain growth is, in the main, achieved in youth and because of the limitation in available young specimens it is not possible to present coefficients for this rapid phase in the growth of the brain.

(b) *Topographical Description.* Figures 7-11. To demonstrate the changes in the skull with age, four skulls were selected which gave a range of size and development

which could be accepted as indicative of increasing age. The skulls chosen were as follows:—

- newborn.* Reg. No. 1965.6.2.1. Known to be newborn.
juvenile. The more complete New South Wales specimen. Chosen on its size and stage of development on generally accepted criteria, such as sutures and occipital crest development.
adolescent. 1959.7.9.2. Chosen on its condylobasal length, small size of ossified scapula and non-fusion of vertebral epiphyses.
adult. 1844.10.5.3. The type of *L. electra* Gray. Chosen on condylobasal length and vertebral and scapular development of a skeleton with skull of comparable size and development (W.A.M. No. 4798).

Cranial Region

General Cranial Shape

- Newborn : The essential cranial shape is obvious, being smoothly rounded from No. 9* foramen magnum to nasals. The lateral development of supra-orbital processes, maxillary plates, and zygomatic processes is slight ; and the supraoccipital crest is not developed. The greatest width of the skull is between the parietals.
 Juvenile : The basic shape of the cranium has already become obscured by the No. 7 extension of the supraorbital and zygomatic processes, incipient post-temporal fossa and occipital crest development. The greatest width is between the zygomatic processes.
 Adolescent : Approximately as in the adult, but the occipital crests are consider- No. 6 ably less developed.
 Adult : The primary cranial shape is very obscured by the growth of these No. 1 various features.

Sutures

- Newborn : All the visible sutures are unfused.
 Juvenile : The only sutures that are fused are those between the occipital bones ; there is partial fusion of the parietals with the supraoccipital ; the interparietal is fused with the supraoccipital.
 Adolescent : There is no significant change from the condition in the juvenile. There is indication however of the beginning of fusion of the nasal portion of premaxillae with maxillae.
 Adult : Nearly every suture has either fused or is showing indication of fusion. The exceptions are : the squamosals which are very loosely joined to the skull ; frontals with maxillae ; jugals with frontals and maxillae ; nasals with interparietal ; vomer with basisphenoids and basioccipital.

* numbers refer to the list on page 177.

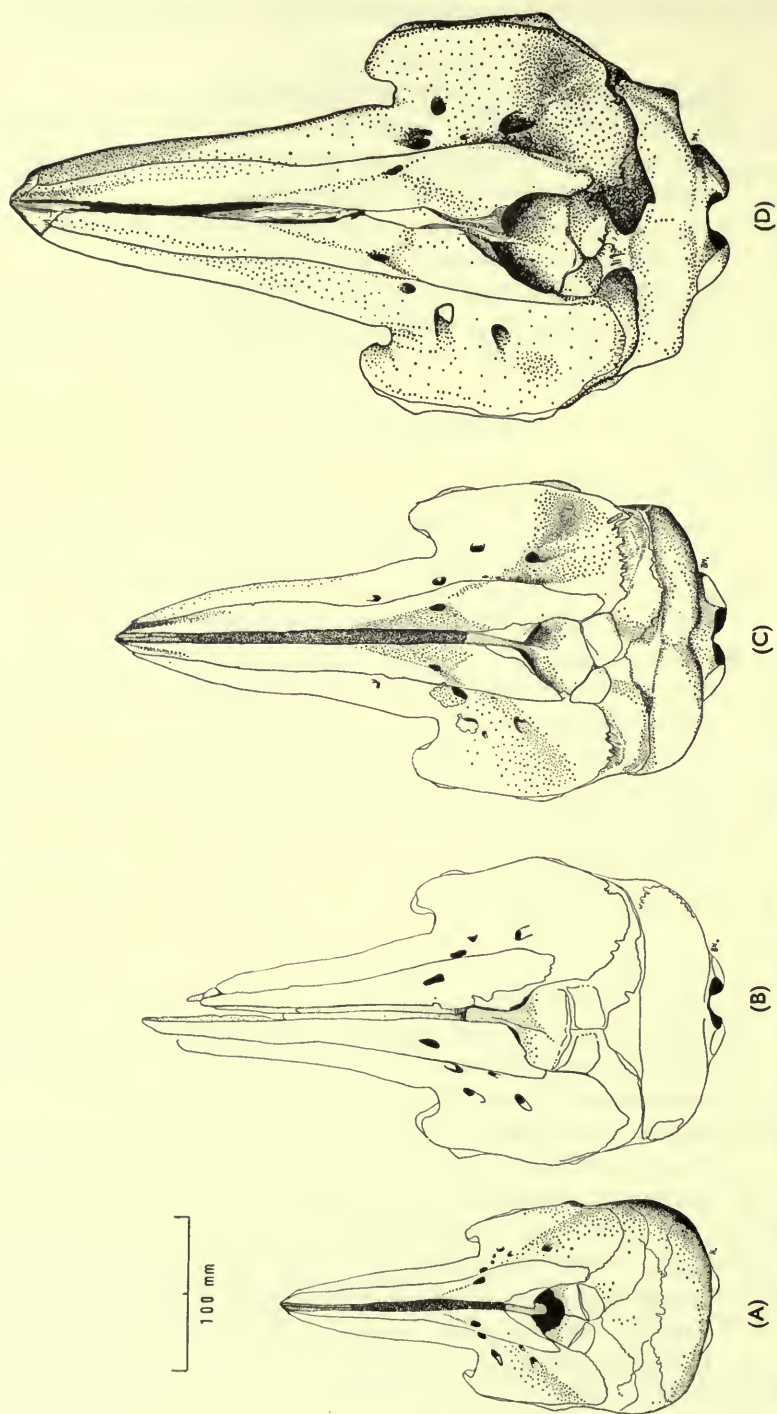


FIG. 7. Dorsal view of skulls of *P. electra*; (A) Newborn, (B) Juvenile, (C) Adolescent, (D) Adult. Orthographic projections.

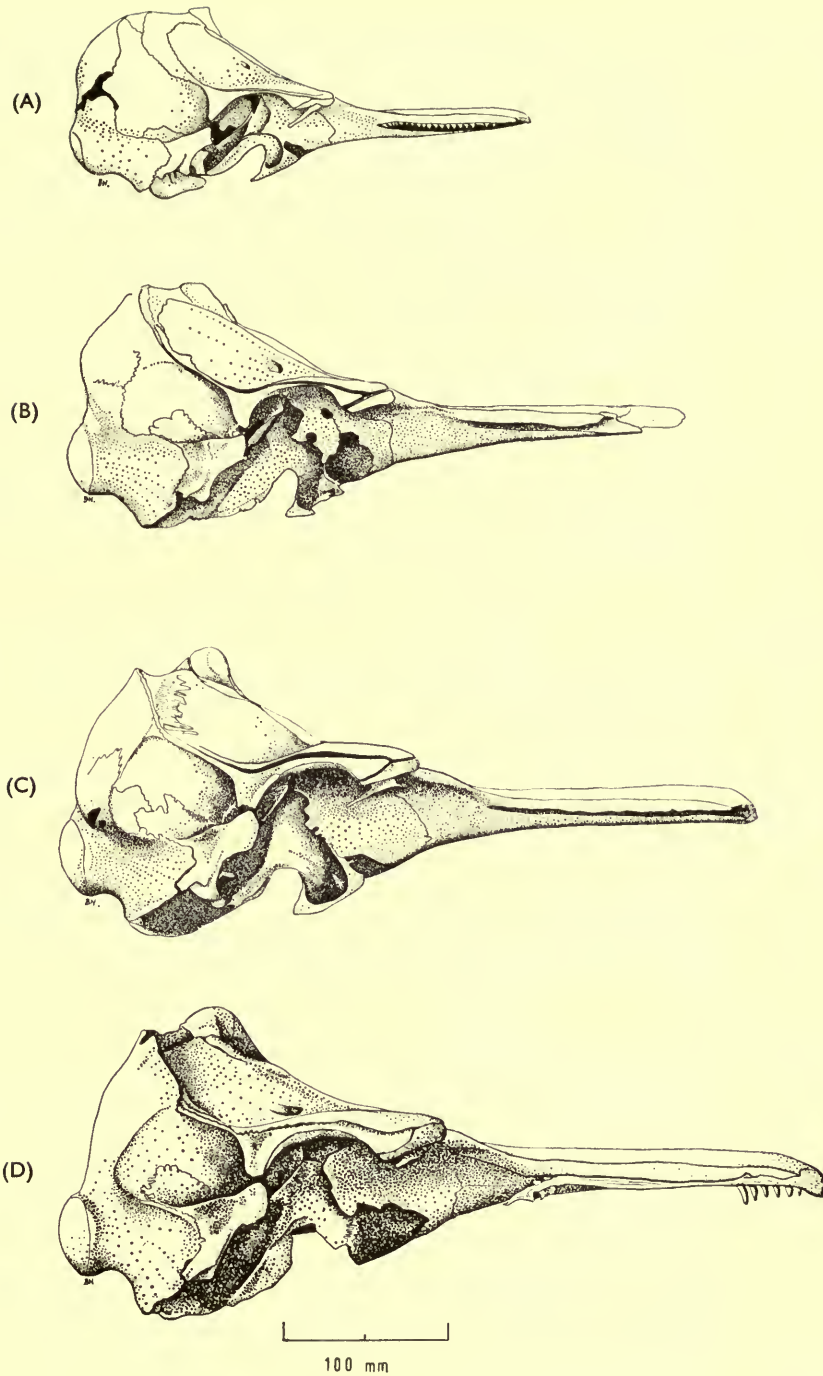


FIG. 8. Lateral view of skulls of *P. electra* ; (A) Newborn, (B) Juvenile, (C) Adolescent, (D) Adult. Orthographic projections.

Development of the mesethmoid

The mesethmoid forms the basal septum and posterior wall of the narial passage.

Newborn : The ossified mesethmoid is present only as a bony stump projecting posterodorsally into a hiatus between the frontals. The nasal septum is composed of soft tissue.

Juvenile : The mesethmoid is considerably more ossified, covering over the hiatus in the cranium, and it has extended appreciably over the frontals. The nasal septum is represented by a bony ridge which has not developed to the level of the dorsal surface of the premaxillae.

Adolescent : The mesethmoid now extends up to make contact with the nasals. The ossified nasal septum is above the level of the lateral borders of the nares. This forward extension however is still restricted and has not yet reached the rostral portion of the skull.

Adult : The ossified mesethmoid has extended into the rostrum and is seen as a flattened plate between the premaxillae. Slightly anterior to the level of the premaxillary foramina the septum becomes cartilaginous and continues so to the rostral tip.

Maxillary Plate

Newborn : The maxillary plates are of reduced extent, their posterior margins being remote from the dorsal margin of the supraoccipital. Their contour anteriorly is much as in the adult but their elevated portions have the contour of the cranium.

Juvenile : The maxillae have grown further back towards the occipital crest.

Adolescent : As in the adult ; but the maxillae have not extended as near to the supraoccipital crest.

Adult : The maxillary plates are spread widely over the frontals. Rostrally they are roughly horizontal, but curve upwards posteriorly toward the vertex of the skull and supraoccipital crest. Frontal is exposed medially between the maxillae and the crests.

Occipital Region

Newborn : The occipital elements are unfused and two large, posterolateral fontanelles are present between the supraoccipitals and exoccipitals. Each fontanelle, in the prepared specimen, communicates with the foramen magnum by a fissure. On the left the fontanelle is partly occluded by a bony centre ; on the right, this is suggested by the sutural margin. The general outline of the occiput is circular, interrupted by the shallow basicranial groove. The foramen magnum is almost piriform in outline ; its continuity is interrupted by the fissures of the fontanelles and the incomplete fusion ventrally of basioccipital,

Juvenile : The supra- and exoccipitals are fused to a great extent. There is a bony insert, which is unfused on the left, in a similar position to

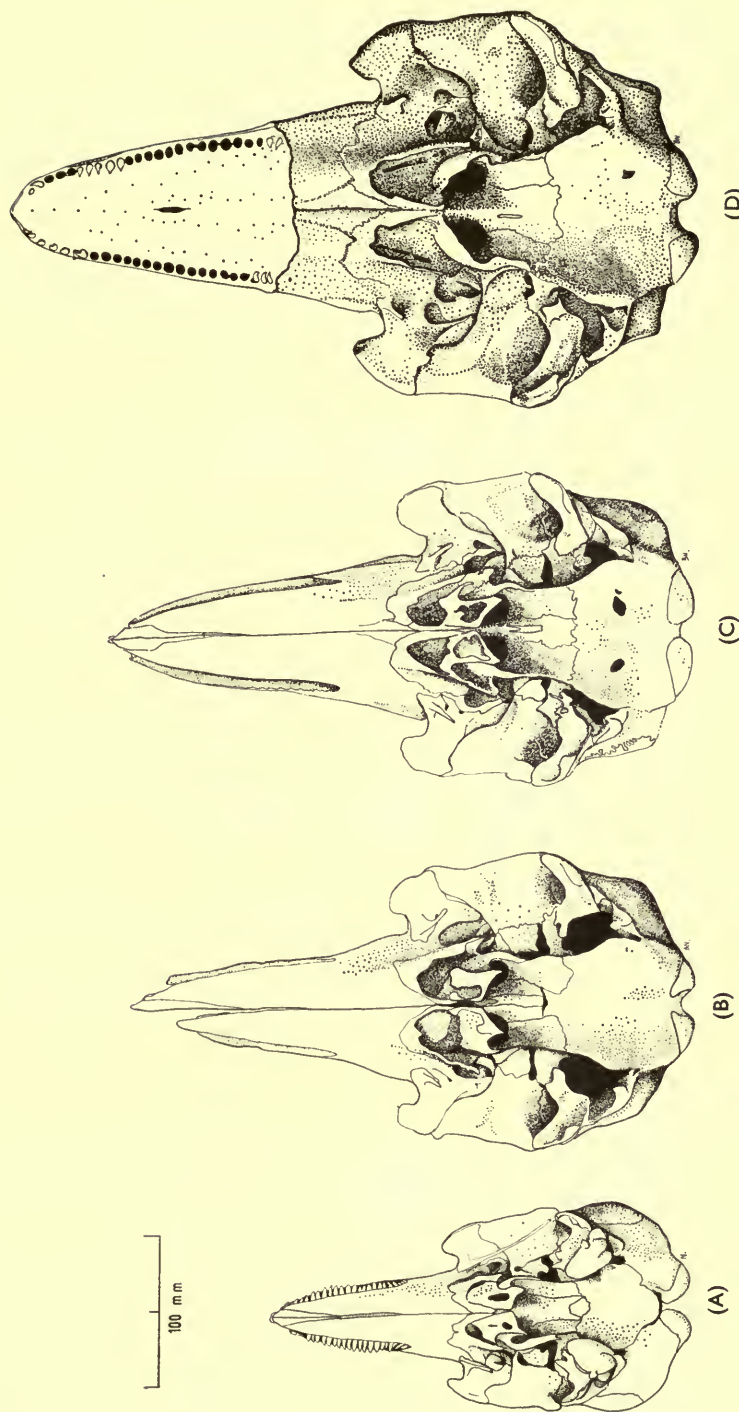


FIG. 9. Ventral view of skulls of *P. electra*; (A) Newborn, (B) Juvenile, (C) Adolescent, (D) Adult. Orthographic projections.

those in the newborn. The postorbital and zygomatic processes are visible beyond the outline of the cranium.

The foramen magnum is subpentagonal, the margin is complete.

Adolescent : Fusion of the sutures is not greatly advanced on the condition in the juvenile. The postorbital and zygomatic processes have increased prominence, and the nasals now appear above the supraoccipital crest. The foramen magnum is more angular dorsally, but more rounded ventrally.

Adult : The occipitals are completely fused, the outline, though generally circular is interrupted by the basicranial trough, postorbital and zygomatic processes. The foramen magnum is regularly oval.

Supraoccipital Crest and Region

Newborn : The crown of the newborn skull shows no evidence of the supraoccipital crest. The supraoccipital, however, abuts on the interparietal medially, and the parietals laterally ; the interparietal is sub-triangular in outline and, with its apex almost touching the right nasal bone, it is in contact with the two frontals anterolaterally, the two parietals posterolaterally and the supraoccipital posteriorly. The maxillae have not extended back into the region of formation of the supraoccipital crest.

Juvenile : The crest is becoming evident. This transverse crest is formed posteriorly by the elevation of the anterior border of the supraoccipital. Anteriorly, in its lateral parts, the posterior borders of the frontals and parietals are involved. Medially, the borders of the interparietal and frontal abut against the supraoccipital margin.

Adolescent : The crest is defined but little developed beyond that of the juvenile.

Adult : The crest traverses the skull coronally in an anteriorly concave arc. It has attained an advanced state of development. In the midline it is connected to the nasals by the isthmus of the nasal boss. It is slightly convoluted over the posterior limit of the frontals.

Post-temporal Fossa

Newborn : The limits of the post-temporal fossa are not defined posteriorly, but its anterior limits are as in the adult. The dorsal surface of the zygomatic process makes an acute angle with the cranial wall of the fossa. The squamous portion of the squamosal is of very little extent. The parietal bone bulges laterally beyond the limits of the zygomatic process and extends high up onto the dorsal surface.

Juvenile : The post-temporal fossa is now defined posteriorly by a low ill-defined ridge on the junction between parietal and exoccipital ventrally, and by a ridge on the parietal dorsocaudally. The dorsal surface of the zygomatic process is now at right angles with the skull ; the

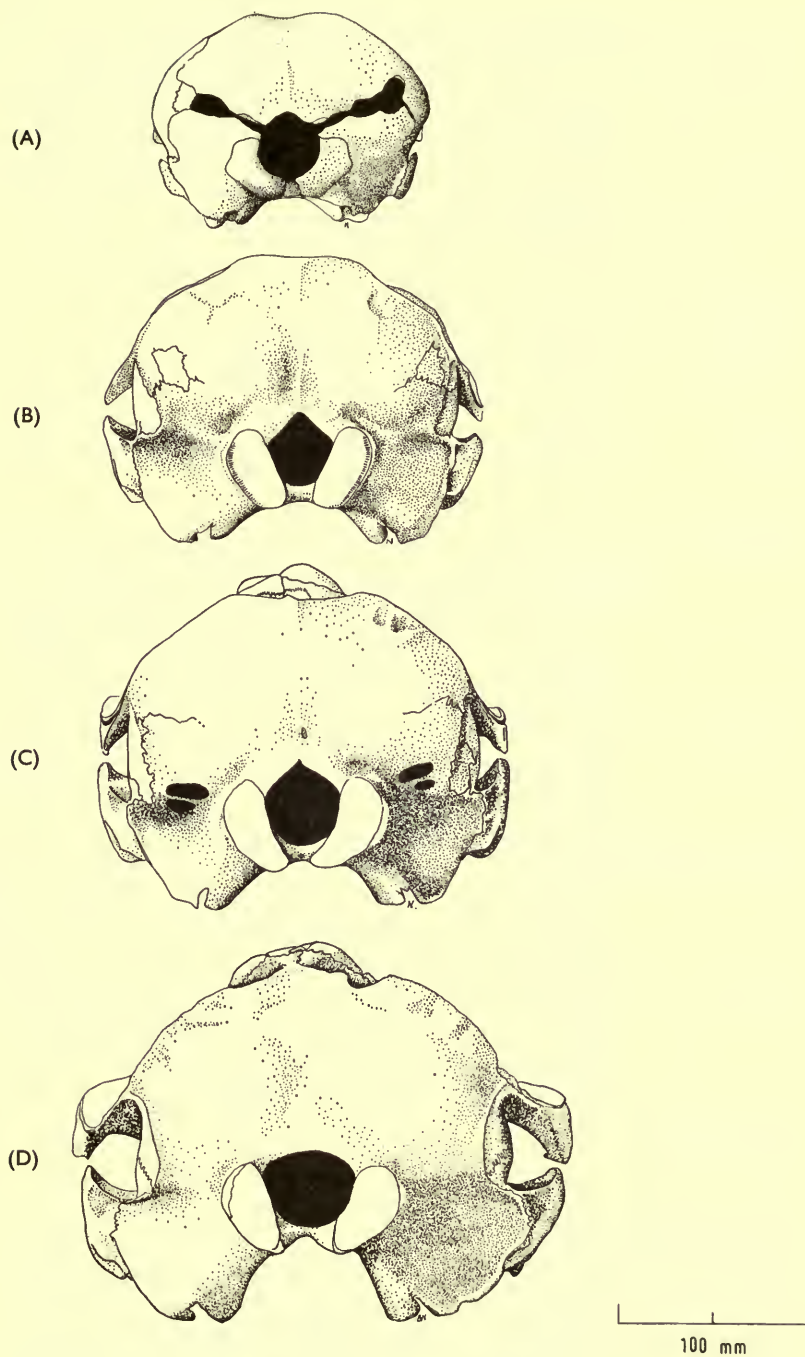


FIG. 10. Caudal view of skulls of *P. electra* ; (A) Newborn, (B) Juvenile, (C) Adolescent, (D) Adult. Orthographic projections.

squamous portion of the squamosal still occupies a relatively small portion of the temporal area.

Adolescent : The post-temporal fossa is clearly defined as in the adult. The squamous portion of the squamosal has increased its area to occupy the lower third of the temporal area.

Adult : There is very little change, except that the ridges demarcating the fossa have become better defined, and the caudal angle has a well defined pyramidal eminence.

Cranial Hiatus

Newborn : Obscured by the ear bones.

Juvenile : There is no secondary bony infilling.

Adolescent : There is bony infilling restricted to the anterior half of the cranial hiatus.

Adult : The cranial hiatus is almost completely filled in by secondary bone.

Basicranial Trough & Crests

Newborn : The trough is comparatively much shallower than in the adult skull. The sutures of basi- and exoccipital are present posteriorly. The junction between basioccipital and basisphenoid has not yet been covered by the backward extension of the vomer, which extends posteriorly as two processes with an appreciable area of basi-sphenoid between them.

Juvenile : The basicranial crests are larger than in the newborn, but they are not adult in size. The posterior extension of the vomer is damaged and is missing to the level of the suture of the basisphenoid with presphenoid, exposing the presphenoid.

Adolescent : The trough is deeper and wider posteriorly, and there has been thickening of the basioccipital part of the crests. The vomer extends posteriorly to the level of the suture between pterygoid/basioccipital/basisphenoid.

Adult : There has been continued thickening of the basicranial crests, but the general size and form shows no change from the adolescent skull. The vomer has grown broader and now occupies a width which is greater than the adjacent pterygoids.

ROSTRUM

a. General

Newborn : The rostrum is much smaller proportionally than the cranial part of the skull.

Juvenile : The rostrum is increasing in size but similar to that of the newborn. (The tip of the rostrum is damaged).

Adolescent : The rostrum is similar to that of the adult but rather more slender.

Adult : The rostrum is robust and in lateral view is wedge shaped proximally, flattening out distally.

b. *Cross Section*

- Newborn : The base of the rostrum is dished, the lateral border of the maxillae is turned up proximally to form a low crest. Anterior to the apex of the prenasal triangle the dorsal surface of the premaxillae is at an angle to the maxillae, the angulation increasing distally to the premaxillary crests.
- Juvenile : The base of the rostrum is dished with the lateral crests more pronounced. The premaxillae have lost their angularity with the maxillae, and posteriorly they have the contour of the adult.
- Adolescent : The base is flatter. The premaxillae are as in the adult.

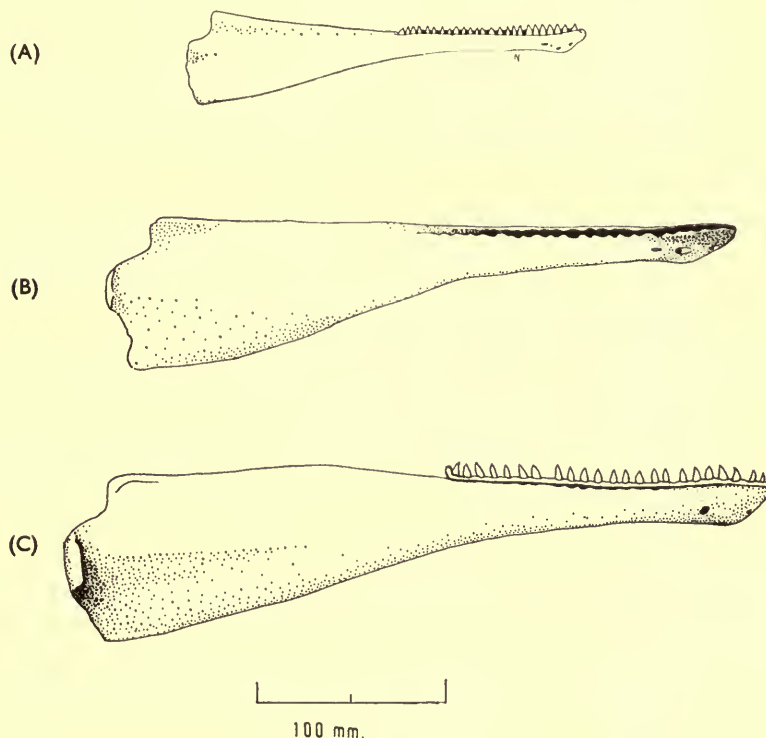


FIG. 11. Lateral view of right mandible ; (A) Newborn, (B) Adolescent, (C) Adult. Orthographic projections.

- Adult : The base is flattened with the lateral margin slightly upturned. The rostrum becomes more convex distally until near the tip, where the regular convexity is interrupted by the flexing of the premaxillae into a pair of crests, which, with the cartilaginous extension of the nasal septum between them, form a blunt keel.

c. *Rostral extension of the Nasal Septum*

This has been discussed in the cranial region.

Tooth Rows and Alveoli

- Newborn : The alveolar grooves form continuous furrows with only the slightest indication of the septa of the alveoli. The teeth are closely set together, and their crowns are exposed to a small extent. The grooves are lateroventrally orientated.
- Juvenile : The alveolar grooves are still continuous furrows, but the individual alveoli are just perceptible by the slightest development of the septa. The grooves are ventrally orientated, but laterally exposed towards the tip. The teeth are missing.
- Adolescent : The alveolar grooves, although continuous furrows, are interrupted lingually and labially by ill-defined alveolar septa. The grooves are more ventrally orientated and the alveoli are more widely spaced. The teeth are missing.
- Adult : The sockets are discrete alveoli. The teeth are separated by a distance of approximately the basal diameter of the teeth. Some teeth are present, and their crowns are not well worn.

LOWER JAW

- Newborn : The general outline is as in the adult lower jaw. The alveolar grooves are continuous, and the teeth are in contact with one another. The crowns have grown above the top of the grooves. The mandibular symphysis is not ossified.
- Juvenile : The lower jaw is missing.
- Adolescent : The same general features as in the adult. The alveoli are defined by the still incompletely ossified septa.
- Adult : The two rami are fused at the ossified mandibular symphysis. The teeth are vertical at the hind end, and splayed out distally. The septa are complete.

NOTES ON THE AXIAL SKELETON

Of the specimens available for inspection three of the skulls had associated vertebral columns :

- Newborn : 1965.6.2.1
 Adolescent : 1959.7.9.2.
 Adult : W.A.M. 4798

There was no axial skeleton to represent the juvenile phase in the comparison. None of the vertebral columns is complete but the portions that were available give information about the development of the axial skeleton ; it was not possible to define the vertebral formula, but Nakajima and Nishiwaki (1965) give it as C_7 (3 fused) + D_{14} + L_{17} + Ca_{44} = 82.

Axial Skeleton of P. electra

- Newborn : The cervical vertebrae of the newborn are all separate. The paired components forming the neural arches of the cervical and the first ten thoracic vertebrae are neither fused with their centra nor with

each other apically. The paired components of the atlas, axis and third cervical vertebra are not fused together (fig. 12). The inferior arch of the atlas is not fused to the centrum of the axis and the latter is still separate from the third vertebra.

The epiphyses of all vertebrae are unfused.

From D.11 the neural arches, while still not joined to their centra are joined apically. Caudally the neural arches are certainly present to the 54th vertebra. All are fused apically and none is fused to its

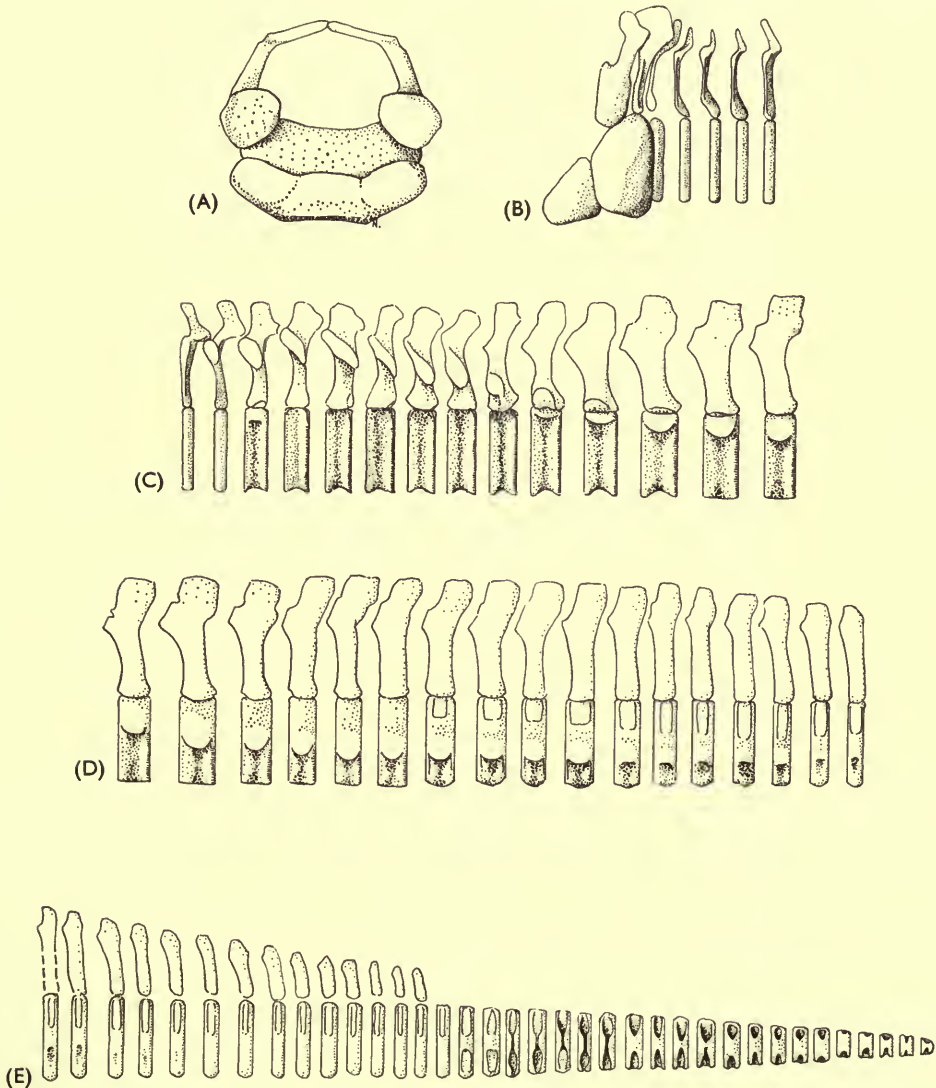


FIG. 12. Semi-diagrammatic drawing of reconstruction of incomplete vertebral column of newborn.

centrum. Incipient transverse processes stem from the neural arches of the first 17 vertebrae, from which point caudally they can be distinguished on the centra, diminishing to disappearance in the posterior caudal region. Rudimentary superior transverse processes are present on the vertebral arches of the 4th—7th cervical vertebrae, but there are no indications of inferior transverse processes.

Adolescent : The atlas, axis and third cervical vertebra of the adolescent are fused ; the atlas and axis being joined at the neural spine and base of the centrum. There is still separation between the neural arches of the atlas and axis dorsolaterally, affording a passage for the second cervical spinal nerve. The third cervical vertebra is fused to the posterior face of the axis, though the limits of the two centra can be discerned. The neural spines of all three vertebrae are fused with each other. The third cervical has an obvious upper transverse process and rudimentary lower transverse process.

The vertebrae are at an advanced state of development ; the vertebral arches are fused to their centra, the transverse processes are well developed. None of the epiphyses of the centra is fused to its centrum. The last 10 vertebrae are missing (from a total of 82 indicated by Nakajima & Nishiwaki, 1965). Neural arches extend tailwards to the 59th vertebra.

Adult : Ventrally, ankylosis of the atlas, axis and third vertebra is more extensive than in the adolescent, but dorsolaterally the limits of the centra of the third cervical vertebra and the axis are still traceable. The neural spine of the axis, which in the adolescent is bluntly pointed, has developed in the adult into a robust spine, terminally bifurcate. The arch of the vertebra is not fused to that of the axis and is incomplete apically. The transverse processes of the axis are rounder, more pointed and extending further laterally than in the adolescent.

The series of vertebrae is not complete, C6 is missing and there are gaps in lumbar and caudal successions, the terminal caudals are all absent. Nevertheless the vertebrae remaining indicate by the absence of unfused epiphyses that the animal was physically mature. The apex of the anticline of the neural spines is at about the 30th vertebra in both adolescent and adult. Post-zygapophyses are present to about the 15th vertebra. The pre-zygapophyses are present on the cervical and anterior thoracic vertebrae, but they are gradually replaced by the increasing prominence of the metapophyses in the anterior thoracic region. The metapophyses in their turn gradually decrease in prominence in the anterior lumbar region, but behind the anticlinal apex they are strongly developed up to the point where the vertebral arches begin to disappear.

Rib Neck Vestiges

The existence of rib neck vestiges on transverse processes has been noted by Flower (1872), Slijper (1936) and Fraser (1940). Slijper notes the condition in *L. albirostris* so far as the genus *Lagenorhynchus* is concerned. The presence of these rib neck vestiges is associated with a change in the attachment of the ribs to the vertebral column. In the adult and adolescent electra there are five and six ribs respectively which possess both capitulum and tubercle. The remaining ribs have neither neck nor capitulum. This change from complete to 'tubercular' ribs is clearly defined on the ribs themselves, but on the associated vertebrae it is expressed as a transitional series, so that if the number of complete ribs is five (as in the adult), the vertebra associated with the sixth rib has attached to it a capitular portion differing very little from that of the preceding rib, except that it is fused to the transverse process and separate from the rib (fig. 13). The heads of the vestiges are in very close proximity to the articular facets on the fifth vertebra, and themselves bear articular facets. The vestige is missing on this vertebra in the adolescent, which has six complete ribs.

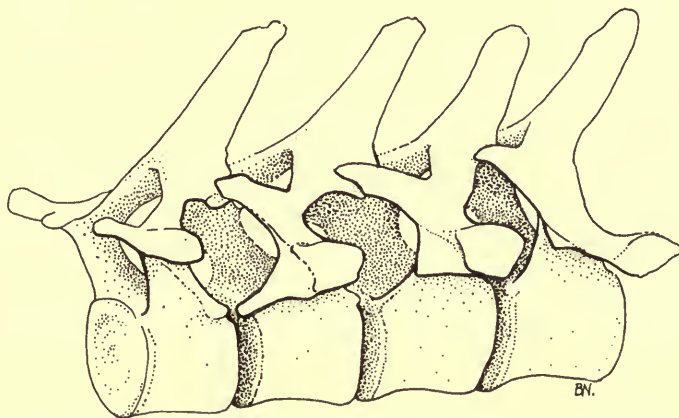


FIG. 13. Anterolateral view of thoracic vertebrae 5-8 of adult, to show the rib neck vestiges.

On the transverse processes of the seventh thoracic vertebra of both the adult and adolescent, there are bilateral, short, hook-like processes whose apices point in the direction the necks of the ribs would follow if present, toward vestigial catapophyses on the vertebra in front.

The vestiges on the eighth vertebra of both the adult and adolescent are low, barely perceptible eminences on the ventral surfaces of the transverse processes. There are very reduced catapophyses on the vertebra in front.

The articular facets for the tubercles of the ribs on the sixth and eighth, and fifth and eighth thoracic vertebrae in the adolescent and adult respectively, are oval, while those of the intervening vertebrae are sub-triangular, implying the incorporation of additional bony elements.

In terrestrial mammals, the majority of the ribs have distinct tubercle and

capitulum. The cetaceans are distinguished by the increased number of ribs having single articulation with the corresponding vertebra. The odontocetes have three patterns of vertebra-rib connection ; anteriorly, a double connection at the head and tubercle with the centrum and transverse process respectively ; further back, a tuberculo-transverse process articulation only ; caudally, there are rib elements which do not have an obvious articulation with the vertebral column. It may be noted further that in odontocetes, the sternal ribs are completely ossified.

The form of double articulation of the ribs with the vertebral column, and possession of ossified sternal ribs anteriorly, indicate the rigidity of the fore part of the rib basket. Posteriorly, the thoracic cage, being without capitular-centrum connections of the ribs and having a much looser association with the sternum, would allow greater flexibility of the body, as pointed out by Slijper.

The connection of the head to trunk demands a strong framework for the relevant musculature, part arising from the vertebral column, part from the ribs, and part from both. Further, the attachment of the pectoral limbs is dependent on muscles arising from anterior vertebrae and ribs, again demanding stability of the rib cage for their proper functioning.

The locomotion of these animals requires a flexibility of the vertebral column and development of axial musculature. This flexibility is initiated in the posterior thoracic region and is achieved by reduction of the vertebral apophyses and development of the inter-vertebral discs ; it seems likely that the removal of the capitular articulation in this region in the vertebral column contributes to this flexibility.

The enlargement of the axial musculature required in connection with cetacean locomotion necessitates a complementary extension of neural spines and transverse processes. In the individual dolphin the progressive lateral extension of the transverse processes of the thoracic vertebrae is unavoidably associated with increasing attenuation of the rib neck. It seems reasonable that a point is reached where the mechanical stability of the neck is lost, resulting in ribs possessing tubercles only.

Summary

Two specimens of dolphin stranded on the coast of New South Wales are identified as belonging to the species *Peponocephala electra*. As Gray's description of the holotype of *Lagenorhynchus electra* is brief, a redescription is given, together with orthographic projections of various aspects of the skull. Ten skulls available for comparison have been measured and the data applied to quantitative assessment of the skull. A topographical survey was made of four skulls of increasing age to show the changes in skull form from birth to physical maturity. Comparative notes have been made of some of the alterations in the axial skeleton with age.

ACKNOWLEDGMENTS

The authors are indebted to Professor Kenneth Norris, University of California, for making available the skeleton of the newborn specimen, Dr. D. L. Ride, Director of the Western Australian Museum for lending the skeleton W.A.M. 4798, and to Dr. R. G. Van Gelder, American Museum of Natural History, New York, for the loan of the specimen A.M.N.H. 4300.

Thanks are due to the many people who wrote or sent photographs relating to the Crowdy Heads school, especially Mrs. W. J. Ward, Mr. H. Anderson and Mr. L. Elford.

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WILLIAM H. DAWBIN, D.Sc.
SCHOOL OF BIOLOGICAL SCIENCES
UNIVERSITY OF SYDNEY
N.S.W., AUSTRALIA

BRUCE A. NOBLE, B.Sc.
c/o BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON, S.W.7

FRANCIS C. FRASER, C.B.E., D.Sc., F.R.S.
c/o BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON, S.W.7



Printed in Great Britain by
Alden & Mowbray Ltd
at the Alden Press, Oxford

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MACROPHTHALMUS (CRUSTACEA:
BRACHYURA) IN THE
COLLECTIONS OF THE BRITISH
MUSEUM (NATURAL HISTORY)



R. S. K. BARNES

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ZOOLOGY

Vol. 20 No. 7

LONDON : 1970

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(NATURAL HISTORY)



BY
RICHARD STEPHEN KENT BARNES

Department of Zoology, University of Bristol

Kref

Pp. 203-251 ; 10 Text-figures

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THE BRITISH MUSEUM (NATURAL HISTORY)
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LONDON : 1970

THE BULLETIN OF THE BRITISH MUSEUM
(NATURAL HISTORY), instituted in 1949, is
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World List abbreviation
Bull. Br. Mus. nat. Hist. (Zool.).

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 28 December, 1970

Price £1.40

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By R. S. K. BARNES

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SYNOPSIS

The British Museum holds twenty three species of the genus *Macrophthalmus* (Crustacea : Brachyura). Nine of these, *M. depressus*, *M. dilatatus*, *M. erato*, *M. grandidieri*, *M. laevimanus*, *M. parvimanus*, *M. pectinipes*, *M. tomentosus* & *M. transversus*, are redescribed and figured. Material from the Royal Society's 1967-1968 Expedition to Aldabra is also included. The convergence with certain sesarmine grapsids displayed by *M. hirtipes*, clinal changes in morphology in *M. dilatatus*, and the systematic value of a number of features of the genus are described and discussed, in addition to a review of the B.M. collection.

INTRODUCTION

THE following is a review of the British Museum collection of crabs of the genus *Macrophthalmus* Latreille (Ocypodidae : Macrophthalminae), it being the fifth contribution towards an eventual revision of this genus (see Barnes, 1966a ; 1966b ; 1967 ; 1968a). The review follows the same basic pattern as that of an earlier paper dealing with the species of this genus from Australia and adjacent regions (Barnes, 1967), and here only those species not covered by that publication will be fully described and figured, i.e. those marked by an asterisk in the list given below. Wherever possible, regression equations have been calculated to show the changes in the carapace length/breadth ratio and that of breadth of front/carapace breadth with changes in size (see Barnes, 1968b).

The collection contains material previously described and discussed by de Haan (1835), Adams & White (1848), Miers (1884 ; 1886), Lanchester (1900a ; 1900b), Laurie (1906 ; 1915), Calman (1927), Gordon (1931), Tweedie (1937) and McNeill (1968). Here, the two hundred and forty four specimens comprising the collected material are assigned to the following twenty three species :

<i>M. bosci</i> Audouin	52	specimens
? <i>M. brevis</i> (Herbst)	16	,,
<i>M. convexus</i> Stimpson	11	,,
<i>M. crassipes</i> H. M. Edwards	8	,,
<i>M. crinitus</i> Rathbun	8	,,
<i>M. definitus</i> Adams & White	6	,,
* <i>M. depressus</i> Rüppell	27	,,
* <i>M. dilatatus</i> (de Haan)	8	,,
* <i>M. erato</i> de Man	9	,,
<i>M. graeffei</i> A. M. Edwards	3	,,
* <i>M. grandidieri</i> A. M. Edwards	10	,,
<i>M. hirtipes</i> (Jacquinot)	8	,,
<i>M. japonicus</i> (de Haan)	10	,,
* <i>M. laevimanus</i> H. M. Edwards	1	,,
<i>M. latifrons</i> Haswell	2	,,
<i>M. latreillei</i> (Desmarest)	22	,,
<i>M. pacificus</i> Dana	9	,,
* <i>M. parvimanus</i> Guérin	1 ¹	,,
* <i>M. pectinipes</i> Guérin	10	,,

¹ Also included in this report are 13 specimens of *M. parvimanus* collected by the Royal Society's 1967-1968 Expedition to Aldabra.

<i>M. punctulatus</i> Miers	.	.	.	.	1 specimens
<i>M. telescopicus</i> (Owen)	.	.	.	.	13 „
* <i>M. tomentosus</i> Souleyet	.	.	.	.	4 „
* <i>M. transversus</i> (Latreille)	.	.	.	.	5 „

The collection therefore contains approximately two thirds of the probably valid species included in this genus. With respect to the validity, or otherwise, of a number of published species, the author has attempted to keep the majority of such discussion for a proposed full revision of *Macrophthalmus*. However, some comments have been made on a number of new synonymies which have become apparent during this study. One particularly difficult case to unravel at this juncture is centred around *M. brevis* (= *M. carinimanus* H. M. Edwards). A considerable number of minor variations and different geographical populations of this species have almost certainly been made the basis for a plethora of specific names, but an adequate treatment of this species must await the examination of more material from more localities. That part of the problem which impinges on *M. dilatatus* has, however, been dealt with in some detail. Other difficult cases are centred around *M. telescopicus* and *M. latreillei*.

In addition, the status of the following species has been deliberately excluded from discussion in this report—*M. consobrinus*, *M. graeffei*, *M. latipes*, *M. milloti* and *M. teschi*.

Any modern worker studying *Macrophthalmus* species from a large geographical area must very quickly become aware that the characters displayed by these organisms do not remain constant, but vary (a) with size of the animal, (b) amongst material from a single locality, and (c) from locality to locality. But as a result of the patchiness of much of the collecting which has produced the specimens examined, our knowledge of many species over much of their range is negligible. In a few cases clinal changes in morphology can be discerned (see *M. dilatatus*) and in more cases intermediate forms between two distinct structural types can be found. But often samples are inadequate for more than tentative judgements.

Complete synonymies are given only for those species not covered by Barnes (1967).

The dimensions given under "Material examined" headings below are of greatest carapace breadth.

A. Subgenus *MACROPHTHALMUS* Sensu stricto

1. *Macrophthalmus (Macrophthalmus) brevis* (Herbst, 1804)

Foreword

This is an extremely problematical species, with an intensely confused synonymy, but since very few specimens have been seen by the author, it would be premature to do more here than indicate the nature and magnitude of the problem.

Six species, *M. laevimanus* H. M. Edwards, *M. sandakani* Rathbun, *M. simdentatus* Shen, *M. malaccensis* Tweedie, *M. malayensis* Tweedie and *M. travancorensis* Pillai, have been described from the area between the Gulf of Manaar and Hainan Island.

Each is known only from one or two localities and between them they total only about twenty specimens. Further, none of these authors refers to any of the other authors' species.

Secondly, there are two very poorly known species, *M. sulcatus* H. M. Edwards and *M. brevis* (Herbst), known from approximately the same area. These eight species, judging from the published descriptions, all appear to grade into one another in a non-linear manner, and there are additional links to a ninth species, *M. dilatatus* (de Haan). Lastly, Lanchester's (1900a) record of *M. crassipes* H. M. Edwards and Tweedie's (1937) record of *M. c.f. crassipes* are not of that species, but together with Lanchester's *M. dilatatus carens* form a tenth unit related to the previous nine. All the material of '*M. brevis*' in the B.M. collection falls into this latter, tenth unit. The status of *M. sulcatus*, *M. sandakani* and *M. malaccensis* will be discussed under the section on *M. dilatatus*, and *M. laevimanus* and *M. malayensis* are considered in a separate section below.

MATERIAL EXAMINED. 8 ♂♂ (12.0–17.0 mm), 8 ♀♀ (11.8–19.7 mm). B.M. Reg. Nos—82.24, 1900.10.22.277–284 (Syntypes of *M. dilatatus carens*), 1900.10.22.285–292.

LOCATIONS. Singapore, Malacca.

COMMENTS. The material with the registration number of 82.24 is that collected by the "Alert" and identified by Miers as *M. dilatatus* (it is not recorded in the results of the "Alert" voyage—Miers, 1884—presumably as a result of an oversight); Lanchester (1900a) regarded it as being identical with his *M. dilatatus carens*. 1900.10.22.277–284 is the type material of the latter subspecies (Lanchester, 1900a), which was considered by Tweedie (1937) to be a series of juvenile *M. brevis*. That with the number of 1900.10.22.285–292 was recorded by Lanchester (1900a) as *M. crassipes*, and Tweedie was of the opinion that, together with his own *M. c.f. crassipes* material, it might form a new subspecies of *M. crassipes* (Tweedie, 1937).

All these specimens are juveniles, which increases the uncertainty of identification. 82.24 and 1900.10.22.277–284 are almost certainly of the same species, to which 1900.10.22.285–292 may belong, but there are a number of noticeable differences between the latter and the two former. What perhaps contributes most to their *incertae sedis* position is that, although juvenile, they are large and possess carapaces relatively longer than would be expected for their size. For example, the largest specimen (19.7 mm) has a carapace length one millimetre larger than that of a "*M. malaccensis*" of carapace breadth 21.8 mm.

2. *Macrophthalmus (Macrophthalmus) transversus* (Latreille, 1817)

Gonoplax transversus Latreille, 1817

Macrophthalmus transversus: Latreille, 1829; H. M. Edwards, 1837; H. M. Edwards, 1852; Cano, 1889; de Man, 1892; Tesch, 1915; Kemp, 1919

MATERIAL EXAMINED. 4 ♂♂ (17.0–23.0 mm), 1 ♀ (18.7 mm). B.M. Reg. Nos—1919.11.91–94, 1951.4.19.2.

LOCATIONS. Chandpur, Balasore (India).

DESCRIPTION. Front deflexed; markedly constricted between bases of ocular

peduncles ; smooth margined ; with almost straight anterior margin and faint median furrow.

Upper orbital border strongly curved, transversely directed ; margin studded with rounded granules increasing in size towards external orbital angle, granules nearest to that angle large and tubercular. Lower orbital border serrated by large, curved, pointed tubercles ; with from three to six very large, more or less flattened spines in centre (each approx. three times longer than normal tubercle and nine times the surface area).

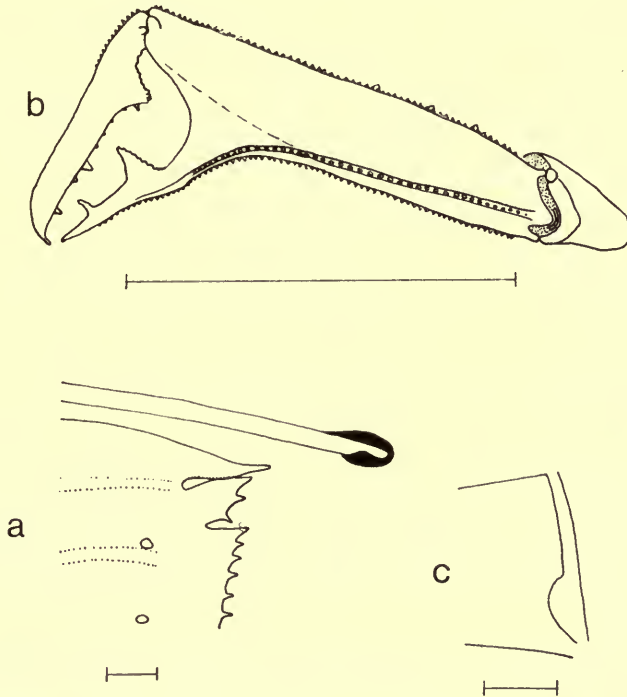


FIG. 1. *M. transversus*—a, anterolateral carapace teeth and ocular peduncle, b, left male chela (outer surface), c, external margin of ischium of external maxilliped. Scale lines a & c 1 mm., b, 1 cm.

Three well defined anterolateral teeth (see Fig. 1a). External orbital angle large, elongate, strongly pointed, directed straight outwards ; anterior margin with continuation of granulation of upper orbital border ; lower margin with rounded granules ; tip often formed by elongate tubercle ; separated from second lateral tooth by deep, narrow incision, wider and more U-shaped in juveniles. Second lateral tooth large, of the shape shown by Fig. 1a, directed outwards and forwards ; anterior margin with rounded granules ; convex or straight outer margin with three large tubercles (in adults), the largest anteriorly forming point of tooth, second in centre of margin, third at posterior angle directed posteriorly ; separated from third lateral tooth by deep, narrow incision. Third lateral tooth moderately large, triangular, pointed,

directed outwards and slightly forwards, with large tubercle at tip ; margins straight, outer margin smoothly continuous with lateral carapace margin.

Carapace completely covered with small, rounded granules ; with well defined, deep furrows ; with well defined, raised clumps of granules on branchial regions, each bearing one very large tubercle in its centre, accessory granules often lacking, "clump" then represented only by tubercle, additional similar tubercle often present between positions of first and second clumps (tubercle formed from second clump) ; with row of four to six smaller, pointed tubercles between branchial clumps or tubercles and lateral carapace margins ; with abruptly sloping sides ; without surface hair. Lateral margins posteriorly convergent, with row of about eight large tubercles on margin, evenly spaced from third lateral tooth to posterior angle of carapace, tubercle at that angle particularly large. With row of granules near to and subparallel with posterior margin. Greatest carapace breadth across external orbital angles. Female carapace without granules excepting on branchial and lateral regions.

Ocular peduncles very long and narrow, projecting beyond external orbital angle for between one tenth and one fifth of their length.

Male cheliped. (a) *Merus*. Upper margin with scattered granules and from one to three large spines centrally ; inner margin with row of tubercles along length, of which any number from two to six may be converted into very long spines (often differentially on the two meri, e.g. one with six, the other three) ; outer margin with scattered granules and one or two large spines distally. Inner surface without granules, with patch of hair centrally and proximally near inner margin ; outer surface with scattered granules near upper and outer margins ; lower surface with scattered granules near outer margin and thickish hair near inner margin.

(b) *Carpus*. Almost hairless. Outer surface with scattered granules, those near lower margin large and tuberculiform ; inner surface more or less smooth, except for a large spine near upper margin and similar spine in central region directed towards palm. Upper margin with scattered small granules ; lower margin with irregular tubercular granules.

(c) *Palm*. Very elongate. Outer surface closely covered with small, pointed granules ; with prominent longitudinal ridge bearing a row of small, pointed tubercles along crest ; anterior margin without notch. Inner surface closely covered with granules, with thick hair over whole surface, with exception of extreme proximal region and area near lower margin, with large spine, and accessory tubercles in large specimens, near to and directed towards carpus. Upper margin with row of from four to eight large spines, increasing in size towards carpus, with granules between spines ; lower margin with pointed granules as on outer surface (see Fig. 1b).

(d) *Index*. Markedly flexed, elongate, very thin. Outer surface with small, sparse granules, with faint, feebly granular continuation of longitudinal ridge of palm, granules decreasing in size distally ; inner surface sparsely granular, with dense hair near cutting margin. Cutting margin with very large, tall, laterally flattened, pointed tooth in centre, tooth either spiniform with straight entire margins, or with a crenulated posterior margin (in some large specimens, the tooth may take the form of two divergent spines joined together at their base), a second smaller spiniform tooth, with entire margins, situated half way between larger tooth and tip of index, re-

mainder of margin usually without further conspicuous granules ; lower margin with pointed granules and few tubercles.

(e) *Dactylus*. Markedly deflexed, elongate, very thin. Outer surface closely covered with small granules ; inner surface completely covered by mat of thick hair. Upper margin with small, pointed granules ; cutting margin with large, triangular, spiniform or crenulated tooth near base, with irregular number of small, cylindrical spines in distal half, with small, irregular granules and tubercles over remainder. Extreme tip of dactylus hooked.

Pereiopod meri with from one to six large spines on the distal part of posterior lower margin in large specimens.

Male abdomen with bulge in morphologically anterior half of lateral margins of sixth segment.

External maxilliped. Internal margin of ischium almost straight or slightly convex ; external margin with a marked and precise concavity proximally (see Fig. 1c), distal portion of margin smoothly but slightly convex. Internal margin of merus convex ; external margin smoothly convex, without differentiated convexities ; anterior margin shallowly concave.

First male pleopod almost straight, without well developed terminal process, without hair on internal margin except at tip.

Central convexity of epistome small and pointed.

DIMENSIONS. Over the size range examined, the carapace length/breadth ratio varies from 0.40 : 1 to 0.44 : 1, and the breadth of front/carapace breadth ratio from 0.12 : 1 to 0.13 : 1.

COMMENTS. *M. transversus*, the type species of the genus, is remarkable for the extremely thin chelae of both sexes (the female chela is as thin as that of the males and possesses similar spiniform teeth, but is otherwise not spiniferous) and for the extremely tubercular and spiniferous carapace, chelipeds and pereiopods, it being rivalled in the latter only by *M. pectinipes*.

As pointed out by Kemp (1919), the additional joint on the dactylus of the male cheliped, as described and figured by Tesch (1915), is the result of a partial fracture of the base of that finger in his specimen.

3. *Macrophthalmus (Macrophthalmus) parvimanus* Guérin, 1834

Macrophthalmus parvimanus Guérin, 1834 : H. M. Edwards, 1837 ; H. M. Edwards, 1852 ; Richters, 1880 ; Miers, 1884 ; Balss, 1934 ; Taylor, 1968

Macrophthalmus convexus kemp Gravely, 1927

Macrophthalmus convexus : Kemp, 1919 (part)

Macrophthalmus consobrinus : Crosnier, 1965

MATERIAL EXAMINED. 7 ♂♂ (8.1–24.9 mm), 7 ♀♀ (10.8–23.3 mm). B.M. Reg. No. 82.24, and Royal Society Expedition, Aldabra 1967–1968 ("Lagoon mud, Dune Jean Louis Creek, Aldabra, 18/xi/1967").

LOCATIONS. Mahe (Kerala), Aldabra.

DESCRIPTION. Front deflexed ; markedly constricted between bases of ocular

peduncles ; smooth margined ; with straight or slightly bilobed anterior margin ; with shallow median furrow.

Upper orbital border curved, markedly backwardly sloping ; margin beaded by small, rounded granules. Lower orbital border serrated by large, evenly spaced, tubercular granules along entire length.

Two well defined and one very poorly defined anterolateral teeth (see Fig. 2a), beaded by small granules along all margins. External orbital angle large, pointed, directed outwards and forwards at its tip ; separated from much smaller second lateral tooth by wide, V-shaped or very narrow incision. Second lateral tooth small, pointed, triangular, directed straight outwards ; separated from third lateral tooth by very small incision. Third lateral tooth very small or absent.

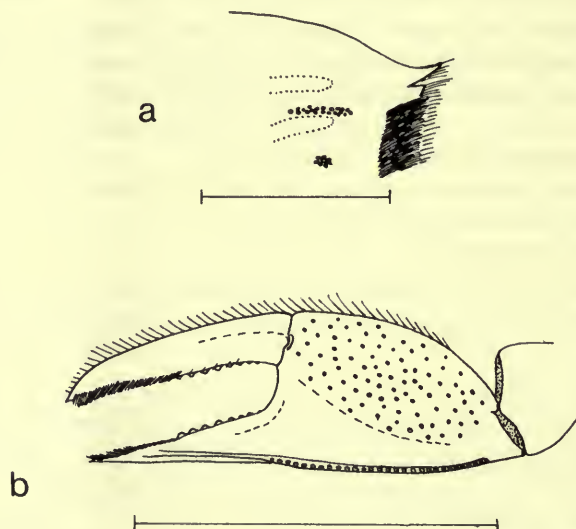


FIG. 2. *M. parvimanus*—a, anterolateral carapace teeth, b, left male chela (outer surface).
Scale lines—5 mm.

Carapace smooth and shiny to naked eye (except for granular clumps on branchial regions), lateral areas microscopically granular ; with faint, shallow furrows, excepting well developed circumgastric ; with well developed granular clumps on branchial regions ; lateral borders with mat of short, fine hair. Greatest carapace breadth across external orbital angles. Lateral margins markedly convergent posteriorly, with rows of long, silky hairs along their length.

Ocular peduncles long and narrow, cornea extending as far as, or slightly beyond, tip of external orbital angle.

Male cheliped. Unique in that it is not sexually dimorphic in this species ; males with small, slender, weak chelae of the same pattern as found in the females of other *Macrophthalmus* species.

(a) *Merus*. Upper and inner margins with long, fine hair ; outer margin with row of very small granules. All surfaces without granules ; scattered hairs only on inner surface.

(b) *Carpus*. Without granules or tubercles. Upper margin with fringe of long hairs ; lower margin with few scattered hairs ; outer anterior margin with long hair mainly in lower portion. Both surfaces smooth.

(c) *Palm*. Outer surface finely granular, with longitudinal ridge very close to lower margin ; inner surface without granules, with square or rectangular patch of short thick hair centrally, with row of long, fine hairs near to and subparallel with upper margin. Upper margin with row of small granules and row of long, fine hairs ; lower margin with small granules on the longitudinal ridge (see Fig. 2b).

(d) *Index*. Undeformed. Outer surface smooth, except for marked, agranular continuation of longitudinal ridge near lower margin, and row of long hairs near distal cutting margin ; inner surface smooth, except for row of long hairs near distal cutting margin. Cutting margin without differentiated tooth except in large specimens, in which from eight to ten granules are associated to form a long, low tooth, from one to two fifths of the length of the margin away from its base, with row of rounded granules proximally ; lower margin smooth.

(e) *Dactylus*. Straight. Outer and inner surfaces smooth, apart from row of hairs near distal cutting margin. Cutting margin without differentiated tooth, except in large specimens in which five or six granules near the base are associated to form a distinct tooth, with few small granules proximally and centrally ; upper margin with fringe of long, fine hair.

Pereiopod meri, carpi and propodi with quite heavily granular surfaces and margins, upper margin of merus with row of hairs, and small subterminal spine.

Male abdomen. Lateral margins of sixth segment with bulge in morphologically anterior position. Sternal surfaces granular.

External maxilliped. Internal and external margins of ischium more or less straight through much of their length, distally convergent. Internal margin of merus convex ; external margin with marked posteroexternal convexity and faint anteroexternal convexity ; anterior margin with shallow concavity.

First male pleopod with very well developed terminal process, without hair on internal margin.

DIMENSIONS. Carapace length = $0.46 \text{ carapace breadth} + 0.82$ (Standard deviation 0.21), Breadth of front = $0.088 \text{ carapace breadth} + 0.59$ (Standard deviation 0.05).

COMMENTS. This species was shrouded in obscurity until the publication of Balss's (1934) paper, in which he showed that there was indeed a species of *Macrophthalmus* with juvenile-like adult male chelae. Previously most authors had accepted Tesch's (1915) contention that *M. parvimanus* was probably based on a female specimen of *Uca*.

M. parvimanus is, in fact, extremely closely related to the well known *M. convexus*, the only character separating the two species being the peculiar cheliped of the former species. The large (32.5 mm), abnormal male recorded by Kemp (1919) from the "upper end of the Gulf of Manaar" is clearly a specimen of *M. parvimanus*. Kemp noted that "The chela differs from that of the female [*M. convexus*] in only two points,—in the possession of rudimentary teeth on the fingers and in the hairy

covering of the inner surface" and that "In all other respects the specimen agrees precisely with normal examples of the species [*M. convexus*]" (Kemp, 1919 : 389 and see his Plate 24, fig. 2). The specimens recorded and described by Gravely (1927) as *M. convexus kempfi*, from the Gulf of Manaar, also belong to this species. Of his specimens, Gravely (1927 : 150) states "As . . . the seven males (two small) in our collection all agree with this abnormal specimen [Kemp's] it is evident that they represent a distinct local race for which I propose the name *kempfi*." Besides the Gulf of Manaar, however, this species is known from the Seychelles (the type locality) and nearby islands, and from Madagascar, since Crosnier's (1965) record of *M. consobrinus* was based on material of *M. parvimanus*. This was ascertained by the examination of part of Crosnier's material in the Muséum National d'Histoire Naturelle, Paris, through the courtesy of Dr. D. Guinot.

4. *Macrophthalmus (Macrophthalmus) dilatatus* (de Haan, 1835)

In this paper, *M. dilatatus* (*sensu* de Haan and subsequent authors) is regarded as the nominal subspecies of *M. dilatatus (sensu novo)* and *M. sulcatus*, *M. sandakani* and *M. malaccensis* are regarded as being synonymous and forming a second subspecies *M. dilatatus sulcatus* H. M. Edwards, 1852 (*comb. nov.*).

a. *M. dilatatus dilatatus* (de Haan, 1835)

Ocypode dilatata de Haan, 1835

Macrophthalmus dilatatus : H. M. Edwards, 1852 ; de Man, 1890 ; Ortmann, 1894a ; Ortmann, 1897 ; ? Doflein, 1904 ; Tesch, 1915 ; Sakai, 1934 ; Sakai, 1939 ; Sakai, 1965

nec Macrophthalmus dilatatus carens Lanchester, 1900a

MATERIAL EXAMINED. 2 ♂♂ (26.3 & 30.8 mm), 1 ♀ (31.5 mm). B.M. Reg. Nos—1935.3.19.37–38, 1961.6.5.92.

LOCATIONS. North China, Tokyo Bay or Sagami Bay (Japan).

DESCRIPTION. Front deflexed ; constricted between bases of ocular peduncles ; with smooth margins, slightly bilobed or straight anterior margin, shallow median furrow.

Upper orbital border markedly curved and almost transversely directed, with little backwards slope ; margin beaded by small, rounded granules. Lower orbital border serrated by large, widely spaced, tubercular granules, often with smaller granules alternating with the large.

Two well defined and one poorly defined anterolateral teeth (see Fig. 3a). External orbital angle narrow, elongate, pointed, directed outwards and forwards to a variable degree (varying from straight outwards to outwards and up to 20° forwards, measured from the transverse carapace axis) ; anterior margin with small granules continuous with those on upper orbital border ; posterior margin smooth ; separated from second lateral tooth by deep, but narrow incision. Second lateral tooth large, wedge-shaped, directed outwards and forwards ; anterior margin smooth or with small granules ; posterior margin straight or convex, with granules ; tip extends as

far as, or slightly beyond, that of external orbital angle ; separated from third lateral tooth by narrow incision. Third lateral tooth variable in size, directed outwards and forwards ; with granular margins.

Carapace of darkish colour, covered with medium sized granules to a variable extent, with central areas almost devoid of granules in some specimens ; with well defined, deep furrows ; with distinct raised clumps of tubercular granules on branchial regions ; with abruptly sloping sides. Greatest carapace breadth across external orbital angles and second lateral teeth, or across latter alone. Lateral margins posteriorly convergent, with rows of hair along length ; posterior margin granular.

Ocular peduncles long and narrow, cornea extending to tip of external orbital angle.

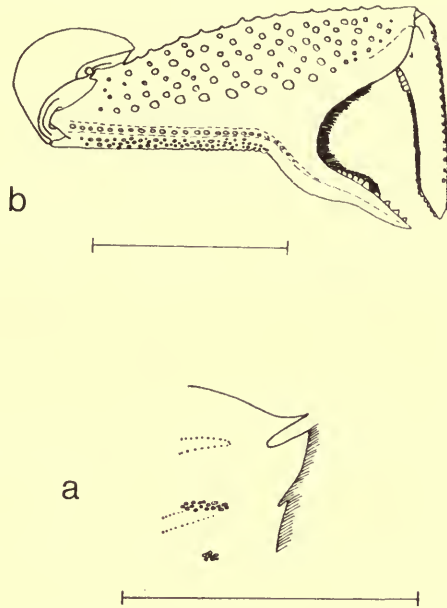


FIG. 3. *M. dilatatus dilatatus*—a, anterolateral carapace teeth, b, right male chela (outer surface). Scale lines—1 cm.

Male cheliped. (a) *Merus*. Upper margin with large tubercle centrally and patch of hair proximally ; inner margin densely haired, with one or two very large tubercles distally ; outer margin granular, with one or two large tubercles distally. Lower surface sparsely granular, with dense mat of hair near and continuous with that on inner margin, hair may extend over most of surface ; inner surface more or less smooth, with hair near inner margin ; outer surface with sparse hair near upper margin and sparse granules near outer margin.

(b) *Carpus*. Almost hairless. Outer surface smooth centrally, with scattered granules near upper and lower margins ; inner surface smooth, except for large tubercle dorsally and similar tubercle centrally near joint with palm. Lower margin with few, large granules distally ; upper margin with sparse row of granules distally.

(c) *Palm*. Elongate. Outer surface with very large, evenly spaced, rounded

tubercles in upper half, the lowest tubercles largest and forming a row (see Fig. 3b), area between row of tubercles and longitudinal ridge smooth, longitudinal ridge prominent and with large granules on crest decreasing in size towards index, area below ridge heavily granular, anterior margin with deep notch ; inner surface heavily haired over all but lower and proximal region, boundary to haired portion marked by row of granules and large spine near to and directed towards carpus, lower proximal region heavily granular, especially near lower margin. Upper margin with row of large tubercles, largest centrally ; lower margin granular.

(d) *Index*. Markedly deflexed in adults. Outer surface more or less smooth, except for low, agranular continuation of longitudinal ridge ; inner surface heavily haired near cutting margin, with small granules near lower margin. Cutting margin with long, low, crenulated tooth occupying proximal half to three fifths, with a few large granules distally in adults ; lower margin granular. In adults, index strongly curved near base, correlated with interdigital notch.

(e) *Dactylus*. Slightly curved, oriented almost vertically in adults. Outer surface smooth apart from row of granules near upper margin ; inner surface heavily haired (hair on inner surfaces of index and dactylus continuous with that on palm). Upper margin granular ; cutting margin with low tooth formed from four or five contiguous granules in a line at base, with rounded granules and dense hair along remainder. Base of cutting margins of index and dactylus widely separate.

Pereiopod meri with hair and small subterminal spine on upper margin, without conspicuous granules.

Male abdomen. Lateral margins of sixth segment with bulge in morphologically anterior half.

External maxilliped. Internal margin of ischium convex ; external margin more or less straight. Internal margin of merus convex ; external margin curving smoothly into anterior margin, without distinct posteroexternal convexity ; anterior margin smoothly concave.

First male pleopod curved, with well developed terminal process, without hair on internal margin except at tip.

DIMENSIONS. Too few specimens have been examined to permit any deductions from their dimensions, but using figures from the literature it can be seen that at a size (carapace breadth) of between 20 and 30 mm the carapace length/breadth ratio is in the range 0.47 : 1 to 0.49 : 1.

b. *M. dilatatus sulcatus* H. M. Edwards, 1852

Macrophthalmus sulcatus H. M. Edwards, 1852 : Alcock, 1900 ; Lenz, 1905 ; Tesch, 1915 ; Kemp, 1919 ; Chhappar, 1957
nec Ortmann, 1894a

Macrophthalmus sandakani Rathbun, 1914 : Tesch, 1918
nec Rathbun, 1924

Macrophthalmus malaccensis Tweedie, 1937 : Crosnier, 1965
Macrophthalmus carinimanus : Lanchester, 1900b

MATERIAL EXAMINED. 3 ♂♂ (21.3–26.3 mm), 2 ♀♀ (19.5 & 23.6 mm). B.M. Reg. Nos—80.6 (part), 1900.12.1.23, 1937.11.15.167–168 (Syntypes of *M. malaccensis*).

LOCATIONS. Santubong, Selangor, "Malaysia".

DESCRIPTION. In this description, only those characters will be mentioned in which *M. dilatatus sulcatus* differs from *M. dilatatus dilatatus* (see above).

External orbital angle small to very small, narrow, triangular, pointed, directed straight outwards, with tip projecting backwards and occasionally across anterior margin of second lateral tooth (in specimens from western part of range, tooth then very small) or with tip projecting outwards and occasionally also slightly forwards (in specimens from eastern part of range, tooth then small), projecting less far laterally than second lateral tooth (see Fig. 4a).

Carapace of lightish colour, completely covered by dense, medium sized granules, without any smooth central regions. Relatively broad (see "Dimensions"), with greatest breadth across second lateral teeth.

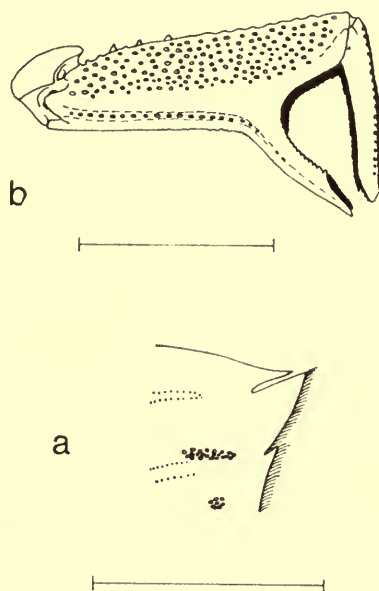


FIG. 4. *M. dilatatus sulcatus*—a, anterolateral carapace teeth, b, right male chela (outer surface). Scale lines—1 cm.

Male cheliped. (a) *Merus*. Upper margin with row of rounded granules along length, without large tubercle; inner margin with four or five very large tubercles centrally and distally.

(c) *Palm*. Outer surface with many, large (but smaller than in the nominal subspecies) rounded granules in upper half, lowest granules not largest and not forming a distinct row (see Fig. 4b).

(e) *Dactylus*. Cutting margin with very small, low tooth, formed from four or five contiguous granules, near base, tooth inconspicuous and often hidden by hair.

DIMENSIONS. Too few specimens have been examined to permit any deductions

from their dimensions, but using figures from the literature it can be seen that at a size (carapace breadth) of between 17 and 26 mm, the carapace length/breadth ratio is in the order of between 0.41 : 1 and 0.45 : 1. Any further data cannot yet be given.

COMMENTS. It will be noticed that these two subspecies differ only in the degree of expression of a few characters. In *M. d. sulcatus*, (a) the external orbital angle is smaller, (b) the carapace is broader, lighter in colour, and more heavily granulated, (c) the tubercles or granules on the outer surface of the palm are smaller and more numerous, (d) the tooth on the dactylus is smaller, and (e) the tubercles on the inner margin of the merus are more numerous and those on the upper margin are not developed, when compared to *M. d. dilatatus*. In addition, the tooth on the index of the westernmost *M. d. sulcatus* is often larger.

Many of these differences of degree, however, appear to vary in a clinal manner, as far as the limitations of the material permit interpretation. In the Japanese material ("*dilatatus*"), the carapace is relatively narrowest, the external orbital angle is largest and directed most forwards, and the tuberculation of the palm is heaviest. In material from Singapore ("*malaccensis*"), the carapace is broader, the external orbital angle is smaller but is aligned in essentially the same direction as in the Japanese forms, although less forwards, and the granulation of the palm is still heavy with traces of alignment of the lowest granules. Thirdly, specimens from India and Mauritius ("*sulcatus*") show the smallest external orbital angles, with the tip directed backwards in some specimens, the broadest carapaces, and the least heavily developed granulation on the palm. Some features of the upper orbital border, the second lateral tooth, and the teeth on the fingers of the male cheliped also show trends consistent with such a clinal change.

Thus the series of "species", *M. dilatatus*—*M. malaccensis*—*M. sulcatus*, shows indications of a continuous change in a number of independent characters from the North East through to the South and West. Even the division into a northern and a southern subspecies may, therefore, be drawing a non-existent distinction, but "*sulcatus*" and "*malaccensis*" at our present state of knowledge appear to be more closely allied to each other than "*malaccensis*" is to "*dilatatus*". Only the collection of more material from the shores of the Bay of Bengal and of the South China Sea will tell whether or not this distinction is valid.

The similarities between "*dilatatus*", "*malaccensis*" and "*sulcatus*" which have led to their being synonymized here have already been described and discussed (see two previous "Descriptions"), there now remains the position of "*sandakani*" and Lanchester's (1900b) record of *M. carinimanus* to be considered. Rathbun's *M. sandakani* was based on a single female specimen from Sandakan, Borneo. Females of the different species within a given subgenus of *Macrophthalmus* are exceedingly difficult to distinguish, females and juveniles often sharing a common structural plan. Hence, separation of the species is usually based on the males. *M. sandakani*, however, does not depart from the structural characteristics exhibited by female specimens of "*malaccensis*", and it does not seem unreasonable, as no evidence to the contrary is apparent, to conclude that they are of the same species. Rathbun (1924) later described a juvenile male of her species from North West

Australia, but this was shown by Barnes (1967) to be almost certainly a young *M. crassipes*.

The material described by Lanchester (1900b) as *M. carinimanus* is in the British Museum, with the registration number of 1900.12.1.23. It is identical to the material described by Tweedie (1937), from a nearby locality, as *M. malaccensis* (Reg. No. 1937.11.15.167-168).

The relationship of *M. dilatatus* (*sensu novo*) to *M. brevis* will not be considered in this paper.

5. *Macrophthalmus (Macrophthalmus) telescopicus* (Owen, 1839)

MATERIAL EXAMINED. 7 ♂♂ (5.6-35.0 mm), 6 ♀♀ (9.0-18.5 mm). B.M. Reg. Nos—83.22, 84.31 (part), 84.31 (part), 1892.4.18.17-20 (part), 1900.10.22.293, 1920.2.23.1, 1934.1.17.132, 1937.9.21.274-275 (part), 1937.9.21.274-275 (part), 1964.7.1.109, & Unregistered.

LOCATIONS. Zanzibar, Sudanese Red Sea, Singapore, Mindano (Philippines), Arafura Sea, Low Isles (Gt Barrier Reef), Torres Straits, Viti Levu (Fiji), Hawaii.

DIMENSIONS. The approximate equations derived from measurements of these specimens are given below.

Carapace length = 0.57 carapace breadth + 0.39, Breadth of front = 0.13 carapace breadth + 0.61.

The breadth of the carapace increases relative to the carapace length with increase in size of these specimens, as in other *Macrophthalmus* species, but contrary to the figures given previously for *M. telescopicus* (Barnes, 1968b). Only small samples have, as yet, been available; further material should resolve this discrepancy.

COMMENTS. The material with the registration number of 1937.9.21.274-275 (part) is that recorded by McNeill (1968), and that with 1900.10.22.293 is that recorded by Lanchester (1900a) as *M. podophthalmus*.

Similar variations in the length of the ocular peduncles and in the relative lengths of the anterolateral teeth to those noted by Barnes (1967) can be seen in the present material. The ocular peduncle projects beyond the external orbital angle for between one half (e.g. 1934.1.17.132 & Unregistered) and one eighth (e.g. 1892.4.18.17-20) of its length, and the external orbital angle : second lateral tooth : third lateral tooth ratio varies from 4 : 2 : 1, through 4 : 3 : 1 and 2 : 1 : 1, to 1 : 1 : 1. Variations in the shape of the tooth on the index of the male cheliped can also be noted.

6. *Macrophthalmus (Macrophthalmus) crassipes* H. M. Edwards, 1852

MATERIAL EXAMINED. 7 ♂♂ (10.7-25.0 mm), 1 ♀ (10.5 mm). B.M. Reg. Nos—1932.11.30.164, 1932.11.30.196-197.

LOCATIONS. Willy Creek & Broome (N.W. Australia).

DIMENSIONS. All the dimensions of these specimens fit the equations given by Barnes (1968b) for this species, to within one Standard Error.

7. *Macrophthalmus (Macrophthalmus) laevimanus* H. M. Edwards, 1852

Macrophthalmus laevimanus H. M. Edwards, 1852

Macrophthalmus malayensis Tweedie, 1937

MATERIAL EXAMINED. 1 ♂ (24.6 mm). B.M. Reg. No. 1937.11.15.166 (Holotype of *M. malayensis*).

LOCATION. Selangor.

DESCRIPTION. Front deflexed ; constricted between bases of ocular peduncles ; with smooth margins, slightly bilobed or straight anterior margin, and shallow media furrow.

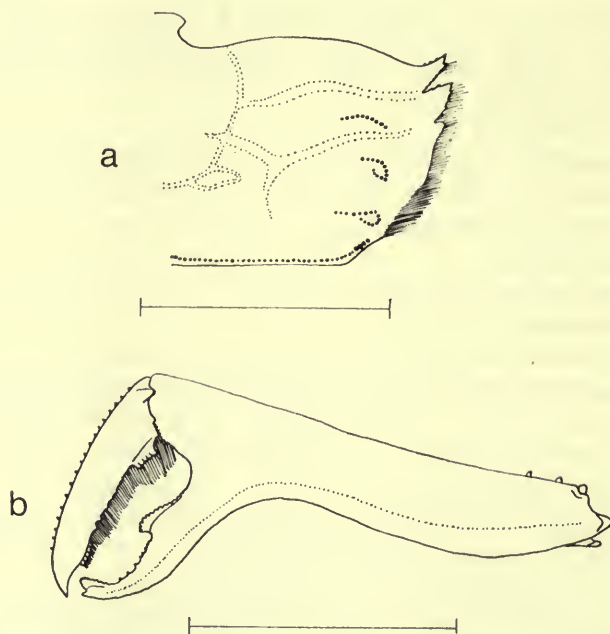


FIG. 5. *M. laevimanus*—a, anterolateral carapace teeth, b, right male chela (outer surface).
Scale lines—1 cm.

Upper orbital border markedly curved, almost transversely directed ; margin beaded by small, rounded granules. Lower orbital border serrated by large, widely spaced, tubercular granules, increasing in size towards external orbital angle, granules nearest external orbital angle, however, small and sparse.

Three well defined anterolateral teeth (see Fig. 5a). External orbital angle narrow, elongate, pointed, directed outwards and forwards at an angle of approx. 40° to transverse carapace axis ; anterior margin with small, rounded granules continuous with those on upper orbital border ; posterior margin with small, pointed granules, except near tip where smooth, granules directed forwards with respect to margin ; tip formed by large granule ; separated from second lateral tooth by wide V-shaped

incision, wider and more U-shaped in juveniles. Second lateral tooth large, wedge-shaped, pointed, directed outwards and forwards, but less forwards than external orbital angle ; anterior margin more or less straight, with pointed granules ; posterior margin convex, with pointed granules ; tip formed by large granule ; separated from third lateral tooth by distinct V-shaped incision. Third lateral tooth small, wedge-shaped, blunt, directed outwards ; with granular margins.

Carapace closely covered with medium-sized granules, largest anteriorly ; with well defined, deep furrows ; with very distinct, markedly raised clumps of tubercular granules, of the shape shown by Fig. 5a ; with abruptly sloping sides ; with row of granules close to and subparallel with posterior margin, of which terminal four or five granules distinctly larger than remainder. Greatest carapace breadth across second lateral teeth ; behind which lateral margins slightly convergent and with row of short, dense hair. Posterior margin smooth.

Ocular peduncles long and narrow ; cornea extending to middle of, or to two thirds the length of, external orbital angle.

Male cheliped. (a) *Merus*. Upper margin finely granular, with large tubercle centrally and smaller tubercle immediately proximal to latter, with patch of hair proximally, with few small tubercles proximal to central tubercle in large specimens ; inner margin with two to four large spines centrally or in distal half, with pointed tubercles over remainder, with long hair centrally and proximally ; outer margin with spine just distal of central, granular proximally, with row of pointed spines or large tubercles distal to spine, decreasing in size distally. Lower surface granular near outer margin, smooth centrally, with scattered hair near inner margin ; inner surface very feebly granular or smooth, with row of long hairs near to and subparallel with central region of inner margin ; outer surface finely granular near outer margin, with sparse scattered hair over more or less smooth remainder.

(b) *Carpus*. Elongate, almost hairless. Outer surface with scattered granules near upper and lower margins ; inner surface more or less smooth, except for two large spines dorsally and similar spine centrally near joint with palm. Lower margin with row of distally directed, pointed tubercles, largest distally, immediately proximal area smooth ; upper margin with one to three pointed tubercles proximal to dorsal spines, with row of distally directed, pointed tubercles distally and centrally.

(c) *Palm*. Extremely elongate in adults. Outer surface with close covering of small granules over whole surface, with very poorly developed granular longitudinal ridge, especially so in adults, without deep, semi-circular anterior notch ; inner surface without hair, with close covering of small granules over whole surfaces, with large spine near joint with carpus. Upper margin coarsely granular, with row of pointed tubercles along length, largest at extreme proximal and distal ends, with the two most proximal tubercles very large and spiniform ; lower margin with granules as on outer and inner surfaces.

(d) *Index*. Markedly deflexed in adults. Outer surface with granules as on that of palm, with continuation of longitudinal ridge only feebly granular ; inner surface with granules as on that of palm, without hair excepting fringe around spooned tip. Lower margin with forwardly directed pointed granules, except at extreme tip ; cutting margin with large wedge-shaped, crenulated tooth occupying proximal half,

with smaller, tall, wedge-shaped, crenulated tooth at extreme tip (see Fig. 5b), with pointed tubercles between the two teeth. Tip of index deflexed upwards, through about 70° in adults.

(e) *Dactylus*. Slightly curved. Outer surface smooth near tip, finely granular over remainder, granules largest near upper and lower margins; inner surface with granules as on that of palm, with mat of hair over all but extreme distal and proximal regions, or over whole surface. Upper margin with rows of pointed granules, largest proximally; cutting margin with large, crenulated, subrectangular tooth near base, with row of large tubercles distal to tooth, the most distal four or five tubercles coalesced in large adults to form a distinct subterminal tooth, extreme tip without tubercles.

Pereiopod meri with very fine hair and subterminal spine on upper margins; upper and posterior lower margins with granules, remainder smooth.

Male abdomen. Lateral margins of sixth segment with bulge in morphologically anterior half. Margins of sternal segments granular near abdomen.

External maxilliped. Internal margin of ischium straight; external margin more or less straight. Internal margin of merus convex; external margin with moderately developed posteroexternal convexity, remainder curving smoothly into anterior margin; anterior margin with slight to moderate concavity.

First male pleopod curved, with well developed terminal process, without hair on internal margin.

COMMENTS. Mme Guinot has been so kind as to forward to the author photographs of the only known specimen of H. M. Edwards's *M. laevimanus*, collected by Leschenault at Pondichery and housed in the Muséum National d'Histoire Naturelle, Paris. These photographs show quite clearly that this specimen is indistinguishable from those described by Tweedie as *M. malayensis*, and hence the two species are here considered to be synonymous.

As stated earlier, comments on the status and affinities of this species will be delayed, pending a re-examination of *M. brevis*.

8. *Macrophthalmus (Macrophthalmus) convexus* Stimpson, 1858

MATERIAL EXAMINED. 8 ♂♂ (14.0–35.5 mm), 3 ♀♀ (8.6–24.1 mm). B.M. Reg. Nos—80.6 (part), 1908.10.27.14–15, 1910.3.29.19, 1929.8.1.11, 1930.12.2.109, 1935.3.19.33, 1950.12.1.22, & Unregistered.

LOCATIONS. Low Isles (Gt Barrier Reef), Torres Straits, Ki Islands (New Guinea), "Malaysia", Hong Kong, S. Formosa, Viti Levu (Fiji).

DIMENSIONS. The dimensions of these specimens fit the equations given by Barnes (1968b) for this species, to within one Standard Error.

COMMENTS. The material with the registration number of 1950.12.1.22 is that referred to by McNeill (1968).

9. *Macrophthalmus (Macrophthalmus) grandidieri* A. M. Edwards, 1867

Macrophthalmus grandidieri A. M. Edwards, 1867 ; A. M. Edwards, 1868 ; Lenz & Richters, 1881 ; Ortmann, 1894b ; Ortmann, 1897 ; Lenz, 1905 ; Tesch, 1915 ; Stebbing, 1917 ; Balss, 1934 ; Monod, 1938 ; Barnard, 1950 ; Fourmanoir, 1954 ; Crosnier, 1965

Macrophthalmus hilgendorfi Tesch, 1915 ; Barnard, 1950 ; Barnard, 1955

Macrophthalmus brevis : Hilgendorf, 1869 ; de Man, 1880 ; Nobili, 1906b

Macrophthalmus carinimanus : Bianconi, 1851 ; Hilgendorf, 1878

MATERIAL EXAMINED. 6 ♂♂ (21.0–29.7 mm), 8 ♀♀ (14.5–28.1 mm). B.M. Reg. Nos—1913, 2, 14, 11–12, 1928.12.1.117–118, 1955.3.5.109–112. (Also examined were four specimens collected by W. Macnae at Inhaca Island, S. Africa, by courtesy of Dr. J. C. Yaldwyn.)

LOCATIONS. Durban, Inhaca Island, Morrumbene Estuary (Mozambique).

DESCRIPTION. Front deflexed ; markedly constricted between bases of ocular peducles ; with smooth margins, slightly bilobed anterior margin, faint median furrow.

Upper orbital border strongly curved and somewhat backwardly sloping ; margin beaded with small granules. Lower orbital border serrated by large tubercular granules, with smaller granules often alternating with the large.

Three well defined anterolateral teeth present (see Fig. 6a). External orbital angle very small, pointed, directed outwards and often backwards so that its tip lies across the middle of the anterior margin of second lateral tooth (see Fig. 6b) ; anterior margin with small granules continuous with those on upper orbital border ; posterior margin smooth ; separated from second lateral tooth by narrow incision. Second lateral tooth very large, wedge shaped, bluntly pointed, directed outwards and forwards ; anterior margin with beading of small granules ; convex posterior margin with large tubercular granules ; tip extends well beyond that of external orbital angle ; separated from third lateral tooth by wide, V-shaped incision. Third lateral tooth relatively large in males, smaller in females, triangular, directed outwards and very slightly forwards, hidden in hair ; anterior margin with thick tuft of hair ; more or less straight posterior margin with few, inconspicuous granules.

Carapace surface covered with small granules ; with well developed, deep furrows ; with somewhat indistinct, but variably developed, raised clumps of granules on branchial regions ; with row of granules near to and subparallel with posterior margin ; with abruptly sloping sides covered with thick mat of hair. Lateral margins posteriorly convergent, hidden under carapace hair. Greatest carapace breadth across second lateral teeth.

Ocular peduncles long and narrow ; cornea not projecting beyond tip of second lateral tooth, but usually beyond that of external orbital angle.

Male cheliped. (a) *Merus*. Upper margin without granules, with patch of short thick hair proximally ; inner margin concealed under thick mat of long hair, without granules ; outer margin covered by large semi-circular granules. Lower surface with thick mat of long hair covering all but small proximal region near outer margin, latter granular ; inner surface smooth on upper portion, covered by mat of hair on lower portion, hair over lower portion of inner surface, inner margin and lower

surface continuous ; outer surface with granules near outer margin, with sparse scattered hair over remainder.

(b) *Carpus*. Almost hairless. Outer surface almost entirely smooth, but with few, very small, scattered granules near upper and lower margins ; inner surface smooth except for large spine centrally, occasionally with one or two smaller tubercles near joint with palm, without tubercle or spine dorsally. Lower margin with small scattered granules ; upper margin with few, small, widely spaced tubercles centrally.

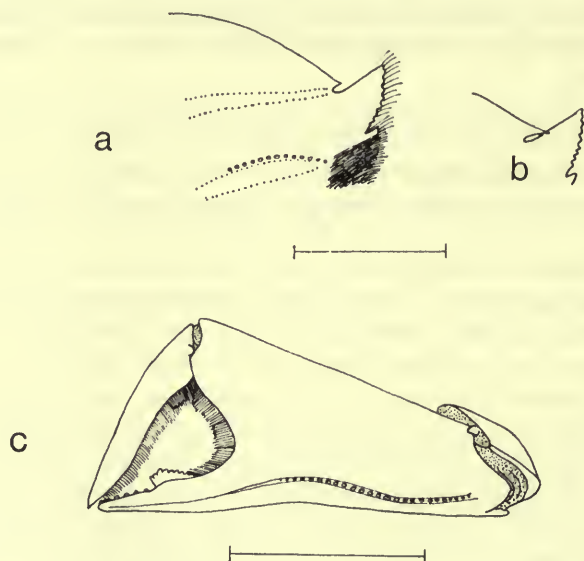


FIG. 6. *M. grandidieri*—a, anterolateral carapace teeth, b, external orbital angle variation, c, left male chela (outer surface). Scale lines—a & b 5 mm, c. 1 cm.

(c) *Palm*. Elongate. Outer surface covered by very fine granules, with prominent longitudinal ridge bearing row of rounded granules along crest (see Fig. 6c), anterior margin with deep notch, height increasing markedly distally ; inner surface heavily haired over upper and distal portion, with fine granules over lower and proximal portion, with large spine near to and directed towards carpus. Upper margin with row of large, pointed, tubercular granules, increasing in size proximally ; lower margin with small granules.

(d) *Index*. Deflexed in adults. Outer surface finely granular, with faint continuation of longitudinal ridge of palm, but without granules on crest ; inner surface heavily haired near cutting margin, finely granular over remainder. Cutting margin with large, crenulated, wedge-shaped or subrectangular tooth in centre, with variable number of pointed tubercles distally ; lower margin finely granular.

(e) *Dactylus*. Slightly curved. Outer surface with fine granules, densest near upper margin ; inner surface heavily haired (hair on inner surfaces of index and dactylus continuous with that on palm). Upper margin with row of pointed tubercular granules along length, on finely granular background ; cutting margin with

large, crenulated, subrectangular tooth near base, completely hidden under thick hair, with small, pointed, tubercular granules distally, margin completely obscured by thick hair.

Pereiopod meri with thick hair along upper margin concealing small subterminal spine.

Male abdomen with slight bulge in lateral margins of sixth segment, in morphologically anterior position.

External maxilliped. Internal margin of ischium convex or almost straight ; external margin convex distally, concave proximally. Internal margin of merus convex ; external margin with slight posteroexternal convexity ; anterior margin shallowly concave.

First male pleopod curved, with flat terminal process, with few hairs on internal margin near tip.

DIMENSIONS. Carapace length = 0.44 carapace breadth + 0.45 (Standard deviation 0.16), Breadth of front = 0.13 carapace breadth + 0.77 (Standard deviation 0.10).

COMMENTS. The synonymy given above follows the opinions of Balss (1934) and Crosnier (1965) with respect to the status of Hilgendorf's (1869 & 1878) and other authors' records of *M. brevis* and *M. carinimanus*, which Tesch (1915) described as a new species, *M. hilgendorfi*.

M. grandidieri is related to *M. dilatatus* and particularly to the southern and western subspecies *M. dilatatus sulcatus*. It differs from the latter principally in the lower degree of carapace granulation, with feebler branchial clumps, and in details of the male cheliped. In the latter, the merus lacks the large tubercles on the inner and outer margins, the carpus lacks the large tubercle on the dorsal portion of its inner surface, the palm lacks the row of granules on the inner surface, and the teeth on the fingers show a number of differences, when compared with *M. dilatatus sulcatus*. The two species are allopatric, *M. grandidieri* replacing *M. dilatatus* in Africa.

10. *Macrophthalmus (Macrophthalmus) graeffei* A. M. Edwards, 1873

Macrophthalmus graeffei A. M. Edwards, 1873a : Ortmann, 1897 ; Laurie, 1915 ; Tesch, 1918 nec Ward, 1928

Macrophthalmus convexus : Tesch, 1915 (part) ; Stephensen, 1945

MATERIAL EXAMINED. 3 ♀♀ (22.0–23.1 mm). B.M. Reg. No. 1934.1.17.133–135.

LOCATION. Sudanese Red Sea.

COMMENTS. As yet no male of this species has been examined by the author, and hence a description of *M. graeffei* and a discussion of its affinities will be postponed. It may be noted, however, that contrary to the opinion of Tesch (1915 ; 1918) it is evidently closely related to *M. telescopicus*, etc., and not to *M. convexus*.

The British Museum specimens are three of those collected on the Sudanese shores of the Red Sea and described by Laurie (1915). In these females, as noted by that author, the ocular peduncles terminate in a small rounded projection distal to the dilated region, wherein would presumably be located the cornea were it not detached

and freely moveable within the peduncle. It is difficult to ascertain from these specimens the shape of the peduncle in life, as the tissue within the cuticle is freely floating in a liquid matrix and the cuticle itself is soft and malleable. It is therefore possible that this terminal projection is an artifact, caused by differential softening of the cuticle, but if it is subsequently found to be genuine it may represent, in a very incipient form, the terminal projection of such species as *Ocypode ceratophthalma* and *Uca stylifera*.

B. Subgenus *MAREOTIS* Barnes, 1967

1. *Macrophthalmus (Mareotis) depressus* Rüppell, 1830

Macrophthalmus depressus Rüppell, 1830 : H. M. Edwards, 1837 ; H. M. Edwards, 1852 ; Heller, 1861 ; Paul'son, 1875 ; de Man, 1881 ; de Man, 1888a ; Henderson, 1893 ; ? de Man, 1895 ; Ortmann, 1897 ; Alcock, 1900 (part) ; Nobili, 1906a ; Nobili, 1906b ; Laurie, 1915 ; Tesch, 1915 ; Kemp, 1919 ; Calman, 1927 ; Gravely, 1927 ; Balss, 1934 ; Stephensen, 1945 ; Barnard, 1955 ; Chhapgar, 1957 ; Crosnier, 1965 ; Macnae, 1968 (part)
nec de Man, 1888b ; Lanchester, 1900b ; Grant & McCulloch, 1906 ; Etheridge & McCulloch, 1916
Macrophthalmus affinis Guérin, 1839a : Guérin 1839b ; H. M. Edwards, 1852
nec Haswell, 1882b

MATERIAL EXAMINED. 17 ♂♂ (7.0–30.8 mm), 10 ♀♀ (8.5–30.9 mm). B.M. Reg. Nos—85.14, 1892.7.15.233–234, 1913.10.30.6–7, 1926.1.26.130–133, 1934.1.17.136–137, 1955.3.5.104–108 (part), 1955.3.5.104–108 (part), 1963.10.24.8.

LOCATIONS. Mozambique, Sudan, Suez, Aden, Persian Gulf, Pamban.

DESCRIPTION. Front deflexed ; constricted between bases of ocular peduncles ; with granular surface, deep median furrow, faintly bilobed anterior margin ; with proximal half of lateral margins granular, remainder smooth.

Upper orbital border curved, slightly backwardly sloping ; margin studded with rounded granules. Lower orbital border with inner four fifths straight and serrated by large, rounded, tubercular granules ; outer fifth abruptly sloping, without granules.

Two large and one small anterolateral teeth (see Fig. 7a). External orbital angle large, broad, rectangular, pointed anteriorly, directed outwards and slightly forwards ; anterior margin with granules continuous with those on upper orbital border ; outer margin with similarly rounded granules ; separated from second lateral tooth by wide, deep, U-shaped incision. Second lateral tooth large, broad, rectangular, directed outwards, projecting beyond former tooth ; anterior and convex outer margins with rounded granules, partly hidden under hair in many individuals ; separated from third lateral tooth by small, U-shaped incision. Third lateral tooth small, triangular, projecting outwards ; outer margin with rounded granules ; hidden under carapace hair in many specimens.

Carapace surface entirely covered by medium sized granules, central gastric region only sparsely covered ; with variable amount of hair (centred mainly in furrows and laterally, but some specimens almost hairless, and others covered excepting central gastric, cardiac and intestinal areas) ; with deep wide furrows, especially circum-gastric, often partly concealed by hair ; with four granular and hairy rows on each

branchial region—transverse row, often inconspicuous, extending across region from level of third lateral tooth, smaller transverse row above insertion of fourth pereopod, two longitudinal rows, inner sinuous, subparallel to each other and to posterolateral carapace margin. Greatest carapace breadth across second lateral teeth, behind which lateral margins parallel or somewhat convergent. Lateral margins with rounded granules and long hairs.

Ocular peduncles long and narrow ; cornea extending to base of external orbital angle.

Male cheliped. (a) *Merus*. All three margins with fine granules completely obscured by thick hair. Inner and lower surfaces completely hidden under thick mats of hair ; outer surface with dense hair near upper margin and scattered hair over remainder. No conspicuous granules on any surfaces.

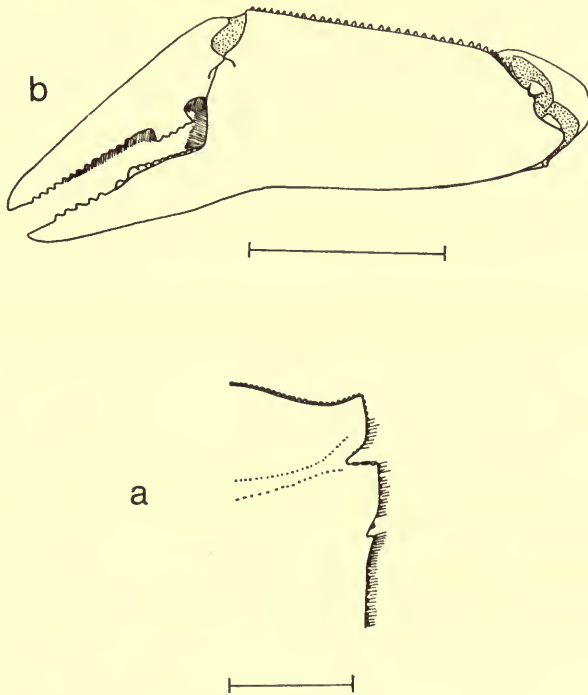


FIG. 7. *M. depressus*—a, anterolateral carapace teeth, b, left male chela (outer surface).
Scale lines—a 5 mm, b 1 cm.

(b) *Carpus*. Elongate. Both margins and inner surface completely obscured by thick mat of hair, beneath which no conspicuous granules. Outer surface finely granular over upper half, smooth over lower.

(c) *Palm*. Moderately heavy. Upper margin with longitudinal row of pointed granules ; lower margin finely granular. Outer surface finely granular, without longitudinal ridge near lower margin (see Fig. 7b) ; inner surface with fine granules completely obscured by thick hair covering whole surface.

(d) *Index*. Deflexed. Outer surface finely granular ; inner surface completely hidden by thick hair, beneath which finely granular. Lower margin with fine granules, densest proximally ; cutting margin with very long, low, crenulated tooth extending from base for a distance equal to more than half the margin's length, distally with rounded or pointed granules.

(e) *Dactylus*. Slightly curved. Upper margin and outer surface finely granular ; inner surface completely obscured by thick mat of hair (hair mats on inner surfaces of palm, index and dactylus continuous) ; cutting margin with large, quadrangular, crenulated tooth near base, with pointed granules distally.

Pereiopod meri with all margins and surfaces hidden by thick hair ; hair also over most carpi and propodi to a variable extent.

Male abdomen. Lateral margins of fourth, fifth and sixth segments almost straight ; surfaces of segments sparsely granular. Anterior sternal segments granular and hairy.

External maxilliped. Internal and external margins of ischium almost straight. Internal margin of merus convex ; external margin with large posteroexternal convexity and much smaller anteroexternal convexity ; anterior margin with moderately developed concavity.

First male pleopod curved ; with well developed terminal lobe ; with sparse hair on internal margin distally.

DIMENSIONS. Carapace length = $0.66 \text{ carapace breadth} + 0.11$ (Standard deviation 0.39), Breadth of front = $0.11 \text{ carapace breadth} + 0.45$ (Standard deviation 0.12).

COMMENTS. This well known species has been remarkably free from controversy, perhaps because the only feature in which it exhibits any marked degree of variation is the degree of carapace hairiness. Kemp (1919) separated a form under the name of *M. teschi* from this species, and the synonymy given above uncritically follows the *status quo* in regarding this species as valid.

2. *Macrophthalmus (Mareotis) japonicus* (de Haan, 1835)

MATERIAL EXAMINED. 7 ♂♂ (15.0–31.0 mm), 3 ♀♀ (11.0–26.1 mm). B.M. Reg. Nos—74.2, 1900.10.22.294, 1926.5.20.5, 1939.3.19.41–42, 1961.3.20.2 (Paratype).

LOCATIONS. Singapore, China (Chekiang, Shantung, Yanghokou), Japan.

DIMENSIONS. In the equations given below, data from the Australian specimens described by Barnes (1967) have been included.

Carapace length = $0.66 \text{ carapace breadth} + 0.38$ (Standard deviation 0.52), Breadth of front = $0.068 \text{ carapace breadth} + 1.13$ (Standard deviation 0.18).

COMMENTS. All these specimens lack hair on the inner surface of the palm of the male cheliped as is typical of this species, whereas the Australian specimens described by Barnes (1967) possess a narrow band of hair in that region. The second described difference between the two forms of *M. japonicus*, that of a continuous, uninterrupted inner longitudinal branchial row in the Australian specimens, is, however, also shown by the North Chinese material (1939.3.19.41–42). It is probable that this structure

is subject to considerable variation over much, if not all, of the range of this species, as found in other members of this subgenus (e.g. *M. tomentosus*). It would be interesting to examine adults of this species from Singapore (so far only juveniles are known) in order to ascertain the hairiness of the inner surface of the palm. In northern forms hair is lacking, whilst it is present in southern specimens.

3. *Macrophthalmus (Mareotis) tomentosus* Souleyet, 1841

Macrophthalmus tomentosus Souleyet, 1841 : H. M. Edwards, 1852 ; A. M. Edwards, 1873b ; de Man, 1888b ; Alcock, 1900 ; Tesch, 1915 ; Kemp, 1919 ; Balss, 1922 ; Tweedie, 1937 ; Sakai, 1939 ; Barnes, 1967

MATERIAL EXAMINED. 2 ♂♂ (24.4 & 32.7 mm), 2 ♀♀ (25.2 & 26.0 mm). B.M. Reg. Nos—86.52, 1935.3.19.45.

LOCATIONS. Mergui, Amoy.

DESCRIPTION. Front deflexed ; constricted between bases of ocular peduncles ; with deep median furrow, sparsely granular surface, straight or slightly convex anterior margin ; with proximal half of lateral margins granular, remainder smooth.

Upper orbital border curved, slightly forwardly sloping ; margin studded with large rounded granules increasing in size towards external orbital angle. Lower orbital border with inner four fifths of margin straight and bearing large tubercular granules increasing in size towards external orbital angle, with outer fifth abruptly sloping and bearing three or four long, low, flattened granules beneath fringe of long hairs.

Two large and one small anterolateral teeth (see Fig. 8a). External orbital angle large, broad, rectangular, pointed anteriorly, directed outwards and forwards ; anterior margin with granules continuous with those on upper orbital border ; outer margin almost straight, with rounded or moderately pointed granules, margins of the two teeth markedly posteriorly divergent ; separated from second lateral tooth by deep, narrow, U-shaped incision. Second lateral tooth very large, very broad, rectangular, pointed anteriorly, directed outwards and forwards ; anterior margin with few or no granules ; outer margin more or less straight, with moderately pointed granules, outer margins of the two teeth markedly posteriorly divergent, so that posterior portion of the tooth projects well beyond anterior portion, which itself projects well beyond external orbital angle (thereby giving a noticeably narrowed carapace anteriorly) ; separated from third lateral tooth by deep, very narrow, U-shaped incision. Third lateral tooth fairly small, broad, triangular, pointed, directed outwards and forwards ; outer margin with granules as on second lateral tooth ; projecting well beyond latter.

Carapace surface, excepting smooth central gastric region, entirely covered with medium sized granules ; furrows indistinct, excepting well marked circumgastric and circumcardiac ; with very poorly defined transverse granular row extending across branchial region from level of third lateral tooth, with well defined transverse row above insertion of fourth pereopod, with two longitudinal granular rows on each branchial region subparallel to each other and to posterolateral carapace margins,

inner row sinuous and often broken in one or two places anteriorly ; posterolateral branchial region with short sparse hair. Greatest carapace breadth across third lateral teeth, behind which lateral margins parallel or even slightly convex (in which case, greatest carapace breadth occurs further posteriorly). Lateral margins with rounded or moderately pointed granules and short hair. Posterior margin granular.

Ocular peduncles long and narrow ; cornea extending to base of external orbital angle.

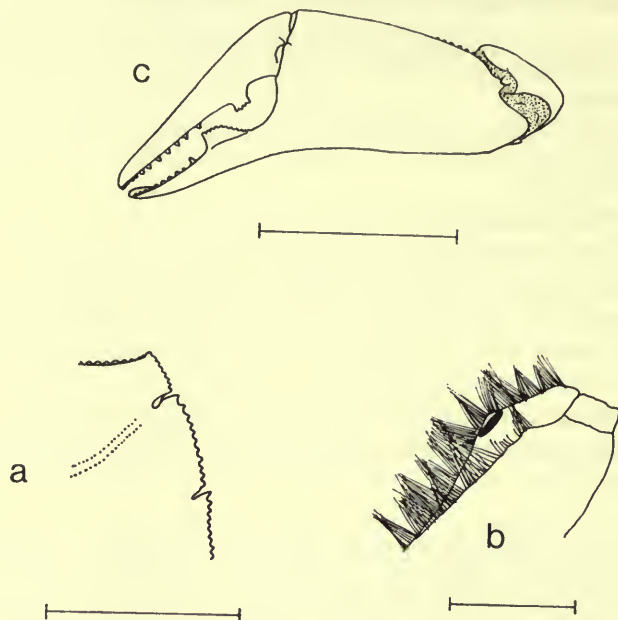


FIG. 8. *M. tomentosus*—a, anterolateral carapace teeth, b, distal region of inner surface of merus of male cheliped, c, left male chela (outer surface). Scale lines—a & c 1 cm, b 5 mm.

Male cheliped. (a) *Merus*. Elongate. Inner margin with row of long hairs ; upper margin with row of pointed granules, largest centrally and distally, and long hairs ; outer margin with scattered pointed granules. Inner surface with row of long hairs near inner margin and diverging from that margin distally, with sparse short hairs over most of surface, with a horny ridge (see Fig. 8b), one eighth the length of the inner margin in length, situated very close to that margin at a distance of about two thirds to three quarters the length of the merus away from the ischium ("musical crest" or "stridulatory ridge") ; outer surface with sparse granules and very short hairs on upper half and near outer margin ; lower surface with scattered granules over half contiguous with outer margin and three large pointed granules near inner margin and ischium.

(b) *Carpus*. Hairless. Upper and lower margins with scattered pointed granules. Outer surface with small pointed granules, except over smooth central area ; inner surface granular and with row of large spines near joint with palm.

(c) *Palm*. Elongate. Upper margin with rows of pointed granules, largest proximally ; lower margin finely granular. Outer surface finely granular, granules largest near upper margin and proximally, without longitudinal ridge near lower margin ; inner surface more heavily granular, with longitudinal row of hairs near upper margin and with sparse mat of short hair over upper distal region.

(d) *Index*. Markedly deflexed in adults. Outer surface finely granular ; inner surface with line of long fine hairs near cutting margin, finely granular proximally, more or less smooth distally. Lower margin finely granular proximally, more or less smooth distally ; cutting margin with large, wedged shaped, crenulated tooth in proximal half (see Fig. 8c), with spiniform tubercles in distal half.

(e) *Dactylus*. Slightly curved. Outer surface finely granular ; inner surface more heavily granular, with mat of very short hair on proximal half near cutting margin and line of long hairs down centre of surface. Upper margin with fine scattered granules, largest proximally ; cutting margin with fairly small, quadrangular, crenulated tooth near base, with row of spiniform tubercles distal to tooth.

Pereiopod meri with thick hair on upper margins and on upper portions of lateral surfaces ; anterior lower margins with medium sized, moderately pointed granules ; posterior lower margins with large pointed granules. Propodi and carpi of second and third pereiopods with mats of hair ; carpi of those appendages with granular ridges.

Male abdomen. Lateral margins of fourth and fifth segments straight, of sixth segment parenthetically convex. Sternal segments granular near abdomen.

External maxilliped. External margin of ischium straight, apart from a distal protuberance at anterior/external margin junction near joint with merus ; internal margin slightly concave. Internal margin of merus straight ; external margin with marked posteroexternal convexity and very small anteroexternal convexity ; anterior margin deeply excised.

First male pleopod slightly curved ; with well developed terminal lobe ; without hair on internal margin except at tip.

DIMENSIONS. Only four specimens have been examined, but these do not depart from the general pattern seen in *Mareotis* and the changes in shape with increase in size will probably be found to be not too dissimilar to the expressions –

Carapace length = $0.66 \text{ carapace breadth} + 1.0$, and Breadth of front = $0.10 \text{ carapace breadth} + 0.25$.

COMMENTS. This is one of the four *Macrophthalmus* species, representing three different subgenera, possessing a horny ridge on the merus of the male cheliped and a specialised series of tubercles on the lower orbital border, which have been suggested to function as a stridulatory apparatus. Although it is difficult to postulate any other function for this apparatus, none of the species concerned have, as yet, been observed or heard stridulating, and no auditory receptors have, as yet, been located (the sound produced, however, may not have an intraspecific function, but may be “directed” towards other organisms).

Morphologically, the most interesting aspect of these structures is their extreme similarity in the four species, which have presumably evolved them independently

(see *M. pectinipes* and *M. erato*), although *M. erato* and *M. tomentosus* may possibly have inherited them from a common ancestor.

4. *Macrophthalmus (Mareotis) definitus* Adams & White, 1848

MATERIAL EXAMINED. 5 ♂♂ (10.0–30.5 mm), 1 ♀ (10.2 mm). B.M. Reg. Nos—43.6 (Holotype), 1930.12.2.215, 1935.3.19.34–36.

LOCATIONS. Philippines, Hong Kong, Canton.

DIMENSIONS. In the equations given below, data from the Australasian specimens described by Barnes (1967) have been included.

Carapace length = 0.68 carapace breadth + 1.33 (Standard deviation 0.98),
Breadth of front = 0.12 carapace breadth + 0.39 (Standard deviation 0.13).

COMMENTS. The male specimen with the registration number of 1930.12.2.215 is that recorded from Hong Kong by Gordon (1931) as *M. teschi* (although with reservations concerning its specific identity). Its assignment to *M. definitus* has also been suggested by Shen (Unpublished B.M. catalogue notes).

5. *Macrophthalmus (Mareotis) pacificus* Dana, 1851

MATERIAL EXAMINED. 4 ♂♂ (15.1–23.3 mm), 5 ♀♀ (16.0–24.5 mm). B.M. Reg. Nos—72.7, 1900.12.1.24, 1908.10.27.12–13, 1930.12.2.211–214, 1935.3.19.43–44.

LOCATIONS. Buntal (Malaysia), Hong Kong, Philippines, Formosa.

DIMENSIONS. The dimensions of these specimens do not depart from the equations already given for this species (Barnes, 1968b) by more than one and a half Standard Errors.

COMMENTS. The specimen with the registration number 1900.12.1.24 is that recorded from Buntal, Malaysia, by Lanchester (1900b) as *M. depressus*. As with the previous species, the identity of this specimen as recorded above was also noted by Shen (Unpublished B.M. catalogue notes).

6. *Macrophthalmus (Mareotis) erato* de Man, 1888

Macrophthalmus erato de Man, 1888b : de Man, 1895 ; Koelbel, 1897 ; Alcock, 1900 ; Rathbun, 1910 ; Tesch, 1915 ; Kemp, 1919 ; Tweedie, 1937 ; Chopra & Das, 1937

MATERIAL EXAMINED. 5 ♂♂ (8.2–13.3 mm), 4 ♀♀ (8.5–13.0 mm). B.M. Reg. Nos—86.52, 1937.11.15.162–165, 1939.3.19.39–40.

LOCATIONS. Mergui, Johore, Canton.

DESCRIPTION. Front deflexed ; slightly constricted between bases of ocular peduncles ; with proximal halves of lateral margins granular ; anterior margin bilobed in males, straight or slightly bilobed in females ; with deep median furrow ; sparsely granular surface.

Upper orbital border strongly curved, slightly backwardly sloping ; margin

studded with small, pointed, slightly curved granules, increasing in size towards and inclined towards external orbital angle. Lower orbital border in males, with 3-5 rounded tubercles on inner quarter of border, tubercles increasing in size towards external orbital angle; with one large triangular protuberance, its apex almost immediately above its internal basal angle and with its height smoothly diminishing towards external orbital angle, occupying central half of border; with one or two small triangular protuberances on external quarter (see Fig. 9a). In females, lower orbital border studded with large tubercular granules along whole length, granules largest centrally.

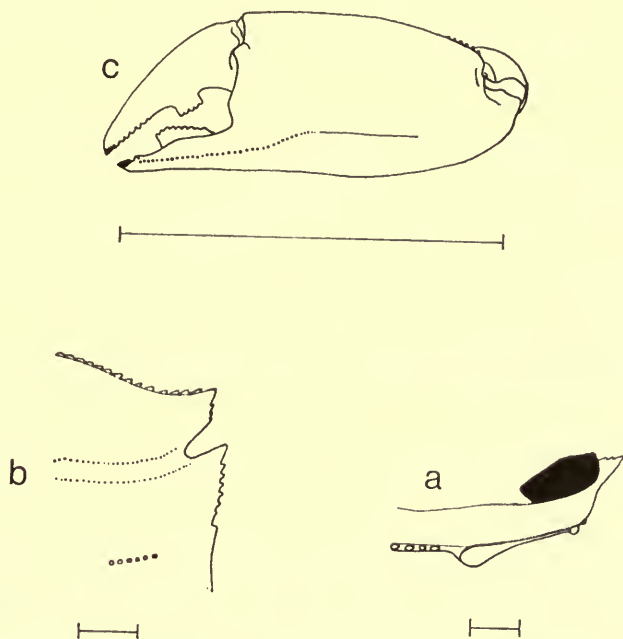


FIG. 9. *M. erato*—a, lower orbital border of male, b, anterolateral carapace teeth, c, left male chela (outer surface). Scale lines—a & b 1 mm, c 1 cm.

Two large and one very small anterolateral teeth (see Fig. 9b). External orbital angle large, broad, subrectangular, directed outwards and forwards, strongly pointed anteriorly; anterior margin with pointed, slightly curved granules continuous with those on upper orbital border; outer margin with a few large pointed granules centrally; separated from second lateral tooth by wide U-shaped incision. Second lateral tooth large, broad, triangular, directed outwards and forwards, projecting beyond external orbital angle, tip strongly pointed; anterior margin smooth or almost smooth; straight or slightly convex outer margin with large, pointed, conical granules along length; posterior half of tooth hidden by carapace hair; separated from third lateral tooth by shallow, almost non-existent, V-shaped incision. Third lateral tooth very small, triangular, with rounded tip, hidden by carapace hair.

Carapace surface covered with small rounded granules, excepting over smooth

central gastric and cardiac regions and over abruptly sloping posterolateral borders, latter covered by thick hair ; with variable amount of scattered hair over remainder out of carapace surface, mainly laterally and in carapace furrows ; with deep distinct furrows demarcating regions ; with convex epigastric ridges, each with row of granules, on each side of median furrow at base of front, in large specimens ; with four indistinct hairy (and sometimes somewhat granular) rows on each branchial region,—very indistinct transverse row extending across anterior branchial region from level of third lateral tooth, short transverse row above insertion of fourth pereopod, and two longitudinal rows subparallel to each other and to posterolateral carapace margins. Greatest carapace breadth across tips of second lateral teeth. Posterolateral margins convex, with row of long hairs concealed by posterolateral carapace hair.

Ocular peduncles long and narrow ; cornea extending to base of external orbital angle.

Male cheliped. (a) *Merus*. Inner margin with series of large pointed tubercles along length, continuing around distal margin of inner surface, tubercles largest distally ; outer margin with series of similar tubercles ; upper margin with series of large, squat, pointed tubercles along distal four fifths of its length, tubercles largest centrally, and with hair on centre of margin, densest proximally. Inner surface without granules, with patch of hair distally, with line of hairs close to and subparallel with inner margin, with short horny ridge of length about one fifth of that of merus situated close to and just distal to centre of inner margin, ridge mounted on flange extending further distally and making an acute angle with plane of inner surface ; outer and lower surfaces covered by thick short hair, lower surface without granules beneath hair, outer surface with few scattered granules near upper margin.

(b) *Carpus*. Upper and lower margins and outer surface coarsely granular, upper margin with two or three large tubercular spines on central region ; inner surface with row of about six large pointed tubercles on crest running up centre.

(c) *Palm*. Upper margin with series of large, squat, conical granules along length, largest centrally ; lower margin with densely scattered point granules. Outer surface closely covered with small pointed granules, without longitudinal ridge near lower margin, but with line of granules in a similar position in some specimens, the line being only just discernible against the scattered granular background ; inner surface covered by thick hair except over extreme lower proximal area, without noticeable granulation beneath hair except near lower margin where heavily granular, with large spiniform protuberance directed at right angles to surface half way between upper and lower margins and about one third the length of the palm from articulation with carpus.

(d) *Index*. Straight, but slightly deflexed at tip. Outer surface with granules as on palm, without longitudinal ridge, but with line of granules along centre of surface showing greater distinctiveness than that on palm with which it is continuous ; inner surface with thick hair, continuous with that on palm, near cutting margin, smooth near lower margin. Lower margin with granules as on lower margin of palm over proximal half, distal half smooth ; cutting margin with large, long, crenulated, subrectangular tooth, of length just less than half that of margin, in a position just

proximal of central (see Fig. 9c), with few conical granules in centre of remaining distal margin.

(e) *Dactylus*. Curved. Outer surface with granules as on outer surface of palm ; inner surface heavily haired, hair continuous with that of palm. Upper margin with densely scattered, small, pointed granules, continuous with those on outer surface ; cutting margin with large quadrangular tooth, one third the length of margin from base, with series of conical granules distal to tooth.

Pereiopod meri with thick hair on upper margins ; upper lateral surfaces of meri, carpi and propodi of third pereiopods heavily haired, similar surfaces of second pereiopods often heavily haired.

External maxilliped. Internal margin of ischium concave ; external margin straight through much of its length. Internal margin of merus convex ; external margin smoothly convex or with posteroexternal convexity ; anterior margin shallowly excavated.

Male abdomen. Lateral margins of sixth segment smoothly convex, of fourth and fifth segments slightly convex or straight.

First male pleopod moderately curved ; with moderately developed terminal lobe, with hair on internal margin distally.

Epistome with straight central region.

DIMENSIONS. Too few specimens have been examined to gain an accurate impression of the changes in various relative carapace proportions with increase in size of the animals. But, as a guide, the regression equations derived from these specimens are given below.

Carapace length = $0.64 \text{ carapace breadth} + 0.71$ (Standard deviation 0.21),
Breadth of front = $0.12 \text{ carapace breadth} + 0.70$ (Standard deviation 0.10).

COMMENTS. In his descriptions of subgenera of *Macrophthalmus*, Barnes (1967) placed this species in the subgenus *Mopsocarcinus*, on the basis of the published descriptions and figures. However, although the central region of the epistome is not at all excavated, the other morphological features of this species indicate a position within the subgenus *Mareotis*. Of particular significance in this respect are the narrow front, hairy branchial rows, the overall shape of the male chela, the lack of a longitudinal ridge on the outer surface of the male palm, the sculpturing of the external maxilliped and the relative sizes of its component segments, and the approximate value of the growth coefficient.

M. erato shows many affinities with *M. crinitus*, and would appear to be a primitive member of its subgenus, as indicated by the straight epistome, the poorly developed branchial rows, the undeflexed index, and the longitudinal row of granules on the outer surface of the palm (which crowns a ridge in species of *Mopsocarcinus*). Comparison between the description of *M. crinitus* given by Barnes (1967) and the foregoing description of *M. erato* shows the extreme similarity of these two species, the most obvious feature separating them being the stridulatory apparatus of the present species. The spine on the inner surface of the palm in *M. erato* is a further distinguishing character, such spines being unknown in other *Mareotis* species and being otherwise known only in species of the nominate subgenus of *Macrophthalmus*.

7. *Macrophthalmus (Mareotis) crinitus* Rathbun, 1913

MATERIAL EXAMINED. 5 ♂♂ (13.6–18.1 mm), 3 ♀♀ (14.8–20.5 mm). B.M. Reg. Nos—1892.4.18.14–16, 1892.4.18.17–20 (part), 1892.4.18.21.

LOCATIONS. Ambon, Ternate, Mindano.

DIMENSIONS. The thirteen specimens of this species known from Australia show changes in their dimensions with size according to the following expressions (Barnes, unpublished).

Carapace length = $0.65 \text{ carapace breadth} + 0.78$ (Standard error 0.17), Breadth of front = $0.12 \text{ carapace breadth} + 0.34$ (Standard error 0.04). These Indonesian specimens differ considerably in their proportions. Their carapace lengths are on average about half a millimetre greater, and their fronts one third of a millimetre broader, than would be expected on the basis of the Australian material. As, however, so few specimens have been examined, little can as yet be concluded from this.

COMMENTS. Other differences between these specimens and the Australian material described previously (Barnes, 1967) can be seen in the structure of the male chela. The juvenile Australian forms possess a longitudinal ridge on the outer surface of the palm and lack a tooth on the index, whilst the only adult examined (13.5 mm) lacked the ridge and possessed a differentiated tooth. The Indonesian forms, although adult and without exception larger than the largest Australian specimen, all show a faint trace of a longitudinal ridge and only the smallest individual possesses a tooth on the index, and then only fully developed on one of the chelae.

C. Subgenus *VENITUS* Barnes, 1967

1. *Macrophthalmus (Venitus) latreillei* (Desmarest, 1817)

MATERIAL EXAMINED. 5 ♂♂ (9.9–44.0 mm), 4 ♀♀ (24.7–45.2 mm), 1 subfossil of unknown sex (c. 38 mm). B.M. Reg. Nos—60.15, 84.31, 1930.12.2.210, 1931.5.15.32, 1934.1.16.162, 1937.11.15.161, 1954.6.24.1.

LOCATIONS. Gulf of Manaar, Bengal ?, Queensland, N.W. Australia, Singapore, Hong Kong, Kobe (Japan).

MATERIAL OF *M. aff. latreillei*. 7 ♂♂ (5.9–21.8 mm), 5 ♀♀ (15.3–19.8 mm). B.M. Reg. No. 1960.6.9.4–10. Philippines.

DIMENSIONS. The dimensions of the above material fall within the range of the expressions given by Barnes (1968b) for this species.

COMMENTS. The variations in structure noted in Australasian material of this species were with respect to (a) the hairiness of the carapace, (b) the tuberculation of the pereopods, (c) the length of the fingers of the male chelae, (d) the pattern of branchial region granulation, and (e) the various changes correlated with increase in size (Barnes, 1967). Comparable variation can be seen in the specimens under consideration here. This is best expressed in tabular form –

Material	Pereiopod tuberculation	Branchial granulation	Carapace hair	Length of fingers
84.31	Absent	Feeble rows	In furrows only	Long
1930.12.2.210	Absent	No rows	In furrows only	Very long
1937.11.15.161	Absent	No rows	Moderately hairy	Short
1931.5.15.32	Marked	Feeble rows	Very hairy	Average
60.15	Absent	Feeble or no rows	Moderately hairy	Moderately long
1934.1.16.162	Absent	Feeble row on 1 side only	Slight	Average

The twelve specimens from the Philippines (1960.6.9.4-10) differ markedly in a number of respects from typical members of *M. latreillei*, these differences being mainly associated with the male cheliped. The palm of the chela is somewhat globose, and the fingers are long (up to half the chelar length), straight, and taper smoothly to a point, the index being inclined upwards in large specimens. The male cheliped is without the thick hair on the inner and outer surfaces of the merus, and on the inner surfaces of the palm, index and dactylus characteristic of *M. latreillei*. The only hair present on the inner surfaces of the chela is a longitudinal row near to and parallel with the upper margins of the palm and dactylus, and a similar row near to and parallel with the cutting margin of the index. The dactylus bears a large, somewhat centrally placed tooth on its cutting margin. In females, the chelae are elongate and of little height. Other differences between the Philippine material and *M. latreillei* are to be found in the anteriorly narrowed carapace, the distribution of carapace hair, the granulation of the posterior carapace margin, and the surface of the third abdominal segment.

Dr. R. Serene has described a number of new species of *Macrophthalmus* in a paper shortly to be published (pers. comm.), and he has kindly provided manuscript descriptions of these species. The 1960.6.9.4-10 specimens clearly belong to one of the new species described by Dr. Serene, and hence they will not be considered further in the present paper.

The material from the Gulf of Manaar (1934.1.16.162) is part of that described and figured by Laurie (1906), and that from Japan (84.31) is part of that discussed by Miers (1886).

2. *Macrophthalmus (Venitus) pectinipes* Guérin, 1839

Macrophthalmus pectinipes Guérin, 1839a : Guérin, 1839b ; H. M. Edwards, 1852 ; Henderson, 1893 ; Ortmann, 1897 ; Alcock, 1900 ; Tesch, 1915 ; Kemp, 1919 ; Chhapgar, 1957
Macrophthalmus simplicipes Guérin, 1839a : Guérin, 1839b ; H. M. Edwards, 1852
Macrophthalmus guerini H. M. Edwards, 1852

MATERIAL EXAMINED. 9 ♂♂ (24.6-73.0 mm), 1 ♀ (40.0 mm). B.M. Reg. Nos—1899.6.17.83-87, 1892.9.16.2-6.

LOCATIONS. Fao (Iraq), Sind (W. Pakistan).

DESCRIPTION. Front deflexed ; markedly constricted between bases of ocular

peduncles ; with smooth margins and surface, markedly bilobed anterior margin, very deep median furrow.

Upper orbital border curved, slightly backwardly sloping ; margin with tall, slender, pointed tubercles, directed somewhat towards external orbital angle, increasing in length slightly towards that tooth. Lower orbital border with about four to six rounded tubercles on inner two ninths of margin ; five or six very large, long, flat protuberances along remainder, inner three or four of which being low triangles in form with rounded apex directly over or very close to inner basal angle of triangle, outer two (i.e. those closest to external orbital angle) more hemispherical ; outer third or quarter of margin with row of hairs (see Fig. 10a) ; in males. In females, inner two thirds of margin with rounded tubercles, outer third with pointed tubercles directed towards front.

Two large and one small anterolateral teeth (see Fig. 10b). External orbital angle large, broad, subrectangular, strongly pointed anteriorly, directed outwards and forwards ; anterior margin with two to four tall, slender, pointed tubercles as on upper orbital border ; tip formed by large, but similar tubercular spine ; outer margin with few, small granules and fringe of long hairs ; posterior margin generally smooth ; separated from second lateral tooth by deep, wide, U-shaped incision. Second lateral tooth large, broad, almost triangular with apex directed outwards, slightly forwards and upwards ; apex formed by large, pointed, tubercular spine ; anterior margin with few rounded granules or smooth ; outer margin more or less straight with evenly spaced, rounded or slightly pointed granules and fringe of long hairs ; separated from third lateral tooth by distinct V-shaped incision (incision and posterior of outer margin obscured by carapace hair). Third lateral tooth small, triangular, pointed, directed outwards and slightly forwards ; outer margin with few rounded granules ; tooth obscured by carapace hair.

Carapace surface with large, tall, scattered tubercles, rounded on central regions and pointed on branchial regions. In adult males, tubercles generally extending over whole carapace, excepting central cardiac and intestinal regions, with a density of approx. 15-20/sq.cm. ; in females and juveniles, tuberculation much less marked, tubercles occurring mainly on branchial regions with only few more centrally. Carapace with deep conspicuous furrows ; with granules on branchial regions ; with thick hair over abruptly sloping sides, hair longest and densest in region of third lateral tooth, and scattered hair in furrows ; without any aggregations of tubercles or granules into clumps and without conspicuous rows of granules, although in some specimens some of the branchial tubercles exhibit some form of longitudinal alignment. Greatest carapace breadth across tips of second lateral teeth, behind which lateral margins subparallel or slightly convergent. Lateral margins with pointed tubercles and row of hairs ; posterior margin smooth or with granules in large specimens.

Ocular peduncles long and narrow ; cornea extending almost to base of external orbital angle.

Male cheliped. (a) *Merus*. Extremely elongate. Inner margin developed into a projecting flange, at right angles to inner surface and continuous in a straight line with plane of lower surface, extending over distal five sixths of margin ; flange of

greatest height at extreme proximal end, tapering smoothly distally ; on crest of flange a horny ridge, one tenth as long as inner margin ; proximal to ridge, margin with few rounded granules and row of long hairs ; distal to ridge, double row of large, pointed, tubercular spines, increasing in size distally. Upper margin with row of pointed granules and row of hairs in proximal half, with scattered granules or smooth

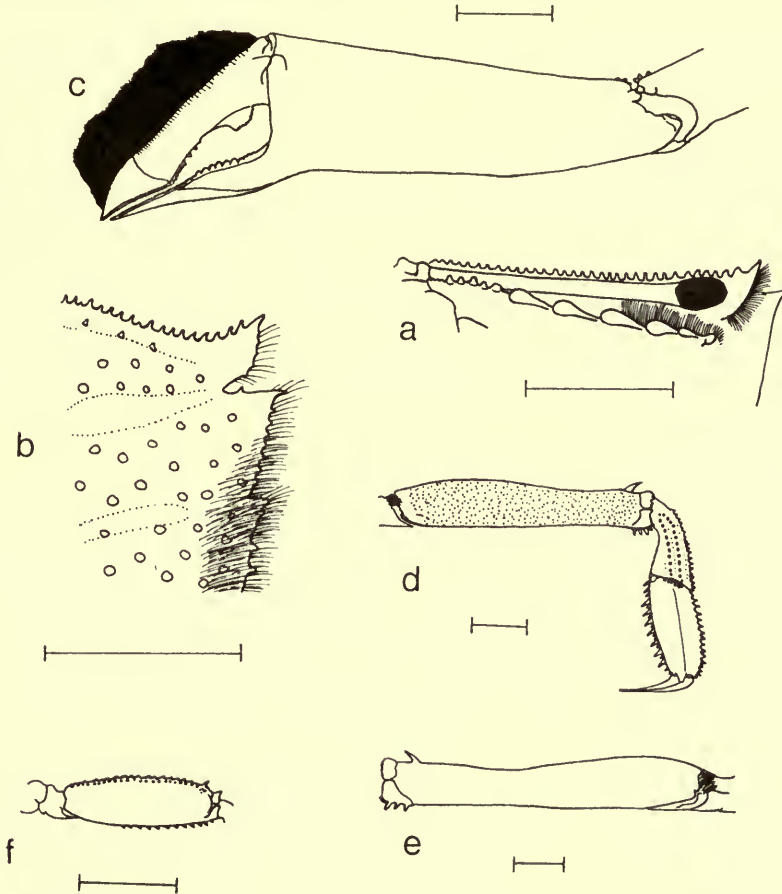


FIG. 10. *M. pectinipes*—a, lower orbital border of male, b, anterolateral carapace teeth, c, left male chela (outer surface), d, third male pereiopod (posterolateral surface), e, merus of third pereiopod of large male (posterolateral surface, with granular detail omitted), f, merus of third pereiopod of juvenile male (posterolateral surface). Scale lines—1 cm.

in distal half ; outer margin with dense pointed granules and from seven to ten large, pointed, tubercular granules in row near joint with carpus. Inner surface with scattered rounded granules over distal two thirds or smooth ; lower surface with pointed granules over outer half, with variable, short, thin hair over underside of flange ; outer surface smooth along central line, with pointed granules and thin short hair near outer margin, with very few small granules and thin short hair near upper margin. Females without flange.

(b) *Carpus*. Upper margin with row of large pointed tubercles ; lower margin smooth. Outer surface smooth, except for a few, small, pointed granules near proximal lower margin and row of similar granules near to and parallel with upper margin ; inner surface with spine near joint with palm, with short fine hair over most of surface, many individuals with scattered pointed granules over upper half.

(c) *Palm*. Elongate. Upper margin with row of broad based, pointed granules, largest proximally ; lower margin finely granular. Outer surface finely granular, without longitudinal ridge near lower margin ; inner surface finely granular, with patch of long hair near distal portion of upper margin, with scattered hair near base of dactylus and above base of index.

(d) *Index*. With extremely elongate tip, deflexed in adults ; with abrupt angulation about half way along the finger in both sexes, so that distal half of index makes an angle of approx. 140° with proximal half, distal half being directed inwards. Outer surface finely granular proximally, smooth distally ; inner surface finely granular, with row of hairs along internal border of markedly spooned cutting margin. Lower margin finely granular ; cutting margin with series of broad pointed granules, joined together at their bases, along anterior half (i.e. as far as angle), forming long low "tooth", distally without granules but with minute serrations in the horny sheath usually found only at the tip of the finger in other *Macrophthalmus* species, but here extending for approx. half the length of cutting margin.

(e) *Dactylus*. With extremely elongate tip ; curved ; with abrupt angulation almost two thirds of length of dactylus from base in both sexes, as on index. Outer surface finely granular, except at tip where smooth, with long hair near upper margin ; inner surface finely granular near base, smooth distally, with scattered hairs over surface and long hair near upper margin. Upper margin with thick mat of very long hair, often extending for a distance greater than height of dactylus above that finger (see Fig. 10c) ; cutting margin with large, long, rectangular tooth, crenulated at tip, near base, distal to tooth with row of granules as far as angle, from angle to tip with minute serrations in horny sheath as on index.

Pereiopod meri of second and third walking legs large, very elongate (especially the third), all surfaces and margins with close covering of large, rounded or pointed granules, without noticeable hair, with a number of large curved spines on distal margins near joints with carpi, largest ventrally. Carpi of first three pereiopods with longitudinal rows of spines along upper (outer) surface (1st carpus with one row, 2nd with one well developed and two moderately developed rows, 3rd with two well developed and one more feeble row – very large specimens with three or four well developed rows) ; carpi of third pereiopod with a few large spines distally on lower (inner) surface near posterior surface of articulation with propodus. Propodi of second and third pereiopods with row of large curved spines along upper margin ; propodi of third pereiopods with row of very large curved spines along lower margin and with mat of short hair over upper half of anterior lateral surface ; mat also extending over much of upper (i.e. outer, as above) half of anterior lateral surface of carpi. Dactyli broad (see Fig. 10d & e). Fourth pereiopod small, with hair fringed margins, excepting lower margins of merus and carpus.

Male abdomen. Lateral margins of fourth, fifth and sixth segments more or less

straight, those of fourth and fifth segments slightly anteriorly convergent, those of sixth parallel. Sixth segment with slight depression in lateral regions near joint with seventh segment, often associated with slight concavity in lateral margins where affected by the depression. Sides of seventh segment slightly concave, segment otherwise a broad based triangle.

External maxilliped. External margin of ischium straight or slightly sinuous ; internal margin slightly concave. Internal margin of merus straight ; external margin with large, flattened posteroexternal convexity, without anteroexternal convexity ; anterior margin shallowly concave.

First male pleopod curved, with very long terminal lobe directed externally at an angle of approx. 75° to the longitudinal axis of pleopod shaft at tip, without hair on internal margin except at tip, external margin and abdominal surface heavily haired.

Central region of epistome straight.

DIMENSIONS. *M. pectinipes* is the largest species of *Macrophthalmus* by a considerable margin, and is probably the largest ocypodid. The largest of the specimens here examined (73.0 mm) had a total span of approx. 30 cm.

As with *M. erato*, the equations given below can only be a guide, as so few specimens have been examined.

Carapace length = $0.56 \text{ carapace breadth} + 0.55$ (Standard deviation 0.34),
Breadth of front = $0.076 \text{ carapace breadth} + 0.65$ (Standard deviation 0.21).

COMMENTS. Juvenile males differ in several respects from the adults. The most marked feature in which they differ is the comparative "normality" of the pereopod meri (see Fig. 10f & c.f. Fig. 10d & e) as opposed to the highly aberrant adult structure. In addition, they show many (*circa* 18) small rounded granules along the inner section of the lower orbital border (i.e. between the epistome and the triangular plates) ; the greatest carapace breadth across the elongate and pointed external orbital angles ; a lack of marked tuberculation on the carapace surface (the smallest male here examined possessed only a number of small tubercles arranged in a longitudinal row on the branchial region in an equivalent position to the inner row of *Mareotis*) ; and the pereopod meri lack the heavily granular surfaces, but possess a row of spines along the upper margin and a similar row along the posterior lower margin of the 2nd and 3rd meri.

As pointed out by Tesch (1915), the variation in the extent of tuberculation of the carapace and the differences observed between the juveniles and adults, and between the two sexes, in this species have resulted in the description of two such morphs as *M. simplicipes* and *M. guerini*.

D. Subgenus **MOPSOCARCINUS** Barnes, 1967

1. ***Macrophthalmus (Mopsocarcinus) bosci*** Audouin, 1825

MATERIAL EXAMINED. 28 ♂♂ (2.5–14.5 mm), 24 ♀♀ (4.5–12.7 mm). B.M. Reg. Nos—81.31, 81.37, 82.24, 84.31, 1937.9.21.270–273 (part), 1937.9.21.270–273 (part), 1937.9.21.270–273 (part), 1937.9.21.270–273 (part), 1951.9.13, 1595.6.22.3–5,

1964.7.10.7-8, 1966.1.24.4-7, 1966.1.24.8-13, 1966.1.24.14, 1966.1.25.15, 1966.1.24.16-20, 1966.1.24.21-25 (part), 1966.1.24.21-25 (part), Unregistered.

LOCATIONS. Inhaca, Mozambique, Dar es Salaam, Mombasa, Red Sea, Monte Bello Is (Australia), Low Isles & Three Isles (Gt Barrier Reef), Queensland, Fiji.

DIMENSIONS. The equations given by Barnes (1968b), slightly modified by the incorporation of data from the above specimens are -

Carapace length = $0.77 \text{ carapace breadth} + 0.21$ (Standard deviation 0.21),
Breadth of front = $0.21 \text{ carapace breadth} + 0.16$ (Standard deviation 0.10).

COMMENTS. The material under the registration number 1937.9.21.270-273 is that collected by the Great Barrier Reef Expedition and recorded by McNeill (1968) under the name of *M. quadratus*. *M. quadratus* is a very inadequately known species, having never been seen since A. M. Edwards (1873b) published his original description of material from New Caledonia. It can, however, be immediately distinguished from *M. bosci* by its possession of a stridulatory apparatus on the lower orbital border and cheliped merus of the male. None of the Barrier Reef specimens possess this apparatus.

2. *Macrophthalmus (Mopsocarcinus) punctulatus* Miers, 1884

MATERIAL EXAMINED. 1 ♂ (7.3 mm). B.M. Reg. No. 81.31 (Holotype).

LOCATION. Port Jackson (Sydney).

E. Subgenus *HEMIPLAX* Heller, 1865

Macrophthalmus (Hemiplax) hirtipes (Jacquinot, 1853)

MATERIAL EXAMINED. 4 ♂♂ (7.3-28.0 mm), 4 ♀♀ (6.2-27.9 mm). B.M. Reg. Nos—84.31, 86.56, 1899.7.18.7-8.

LOCATIONS. Dunedin, Queen Charlotte Sound (New Zealand).

DIMENSIONS. The above specimens fit the equations given by Barnes (1968b) within two Standard Errors (length : breadth) and one Standard Error (front : breadth).

COMMENTS. A point of great interest with respect to the subgenus *Hemiplax* is the great similarity displayed by this group to certain sesarmine grapsids, particularly to those of the genera *Metaplax* and *Helice*. This resemblance must have been apparent to Heller (1862), since he described specimens of this species as a new form of *Metaplax*! The similarity is displayed by (a) the shape of the front, (b) the carapace shape, and particularly the shape of the anterolateral teeth, (c) the short, stout ocular peduncles, (d) the shape of the central region of the epistome, (e) the presence of an oblique row of granules on the branchial region of the carapace, extending from the posterior region of the third lateral tooth to a position above the insertion of the fourth pereopod, the rows on the two branchial regions converging posteriorly (this oblique row in *Hemiplax* is not found in other *Macrophthalmus* species), (f) the presence of a transverse granular row extending across the branchial

region from the tip of the third lateral tooth, and a concave granular row immediately above the fourth pereopod insertion, and (g) the breadth of the sixth abdominal segment markedly exceeding the breadth of the base of the seventh segment (again not occurring in other *Macrophthalmus* species).

By virtue of its gross external morphology, *Hemiplax* is, therefore, likely to be confused with these Sesarminae. The structure of the male chela and of the external maxilliped, however, show typical *Macrophthalmus* patterns and depart radically from those of the Sesarminae; its true affinities are also shown by a number of other features in which these grapsids and the Macrophthalminae differ.

It can be seen that, in general, *Hemiplax* has approached the grapsid pattern of gross external morphology, rather than vice versa, which raises the question of why these ocypodids should have evolved such a similar facies to the sesarminae. Answers to such a question can only be sought by a close examination of the ecology and behaviour of the relevant species, the convergent modifications being mainly associated with burrowing and respiration (Garstang, 1897; Verwey, 1930). Undoubtedly, however, the geographical isolation of the *Hemiplax* species from their congeners has been a factor of major importance in their evolution. *M. hirtipes* is, for example, the only ocypodid crab in the New Zealand fauna, and it may be significant that the sole New Zealand ocypodid should so greatly resemble the more plentiful, and presumably more successful, grapsids.

Only two other known species are referable to the subgenus *Hemiplax*: *M. major* (Glaessner), a large (c. 52 mm), subquadrate carapaced species known only from the Lower Pleistocene of New Zealand, and *M. boteltobagoe* (Sakai), known only from one specimen from Formosa. A third species, as yet undescribed and known only from a Pliocene cephalothorax from New Zealand, may be referable to this subgenus (Glaessner, 1960). Therefore only one *Hemiplax* species is known from a region other than New Zealand, and from a region in which other members of the Ocypodidae are also present. Serene (pers. comm.), however, is of the opinion that *M. boteltobagoe* should be assigned to *Mopsocarcinus* and not *Hemiplax*, and if he is correct *Hemiplax* species are known only from New Zealand, a region lacking in other ocypodids.

F. Subgenus **TASMANOPLAX** Barnes, 1967

Macrophthalmus (Tasmanoplax) latifrons Haswell, 1882

MATERIAL EXAMINED. 1 ♂ (24.0 mm), 1 ♀ (21.5 mm). B.M. Reg. No. 1955.3.4. 1-2.

LOCATION. Westernport (S.E. Australia).

DIMENSIONS. The measurements of the above specimens agree, to within one Standard Error, with the expressions given for this species by Barnes (1968b).

DISCUSSION

Descriptions of sixty six different species of crabs referable to *Macrophthalmus* may be found in the literature, of which ten were based on fossil or subfossil remains.

Of one species, *M. laevis* A. M. Edwards, almost nothing is known. Twenty five of the remaining sixty five have been reliably shown to be synonyms, leaving twenty seven probably valid species (including three known only from fossil material) and thirteen doubtful species, of which only between three and six are likely to be valid. This gives a total of between thirty and thirty three valid *Macrophthalmus* species and of between twenty seven and thirty living species (and to the author's knowledge a further five new species are at the moment "in press").

As the author has now examined twenty four of these species, this is a suitable moment to briefly consider what characters are of use to the systematist working on this genus.

Two characters, much used in other brachyuran groups, are of little or no importance in *Macrophthalmus*. These are the morphology of the first male pleopod and colouration, which in this genus is uniform and drab effecting concealment against the uniform, drab background of the frequented mud and sand flats. Excepting the two basic divisions into which the Macrophthalminae can be partitioned (see Barnes, 1967 : 201), which are well characterized by differences in gross pleopod morphology (and for which 'Linearipleopoda' and 'Curvipleopoda', for *Macrophthalmus*, etc., and *Cleistostoma*, etc., respectively, would be apt names at the tribal level), differences between the pleopods at the subgeneric and specific levels are trivial and dwarfed by differences shown by other skeletal elements.

At the subgeneric level, several gross differences in major structural components are apparent. These are : (a) the relative breadth of the front, and to some extent correlated with this the length and cross-sectional diameter of the ocular peduncles, e.g. the growth coefficient of the front as compared with the carapace breadth is c. 0.29 in *Hemiplax*, c. 0.22–0.23 in *Mopsocarcinus*, c. 0.09–0.16 in *Macrophthalmus* (*sensu stricto*), and within the latter range in the three other subgenera ; (b) the length/breadth ratio of the carapace, e.g. the growth coefficient of the length as compared with the breadth is c. 0.43–0.46 in *Macrophthalmus* (with the exception of *M. telescopicus*), c. 0.64–0.68 in *Mareotis* (with the exception of *M. setosus*), and c. 0.70–0.78 in *Mopsocarcinus* ; (c) the presence or absence of granular rows or clumps on the carapace ; (d) the gross form of the anterolateral carapace teeth ; (e) the shape of the central region of the epistome ; (f) the sculpturing and relative sizes of the merus and ischium of the external maxilliped ; (g) the presence or absence of a longitudinal ridge on the outer surface of the male chela, and a number of other features of gross chelar form ; (h) the size and tuberculation of the pereopods ; and (i) the shape of the sixth abdominal segment in the male.

The majority of these subgeneric points of difference are those of gross carapace morphology and can be seen in both sexes. They are probably related to the different environments frequented by the different subgenera. For example, *Mareotis* species most commonly occur in predominantly muddy substrates and are frequently estuarine, whilst *Macrophthalmus* (*sensu stricto*) species most commonly occur in substrates containing a fair percentage of 'sand' and are less frequently estuarine (for that reason, if for no other), and *Mopsocarcinus*, of which all species are relatively small, often occurs under stones, etc. Many of the areas of difference enumerated above can be correlated with the demands made on the systems of feeding, burrowing,

respiration, etc, by the various substrates, with due regard for the size of the animal concerned.

Specific differences within the subgenera are of a very different nature. Some species are characterized by the markedly atypical character of one or more structures, e.g. the greatly elongated ocular peduncles of *M. transversus* and *M. telescopicus*, but most species can only be separated with confidence on features shown solely by the male sex. These differences are mainly ones of ornamentation patterns on the cheliped, but again some species can be characterised by the possession of markedly atypical features, e.g. the thin chelae of *M. transversus*, the non-dimorphic chelae of *M. parvimanus*, and the stridulatory apparati of *M. tomentosus*, *M. erato*, *M. pectinipes* and *M. quadratus*. But before discussing the nature of the specific differences exhibited by the majority of species, brief mention will be made of those features of the morphology of *Macrophthalmus*, which, although they are within certain limits modified in different directions by different species, are subject to considerable variation within a number of individual species and are therefore dubious characters upon which to base specific distinctions, especially if only limited material is available.

Characters subject to variation in *Macrophthalmus* are of three types,—those showing sexual dimorphism, those varying with size of the animal, and those exhibiting differences amongst animals of the same size and sex in a single population (often in practice from a single locality) or in geographically separated populations. The first and second types show many similarities, since juvenile males show many resemblances to adult females, but small and large adult males also often differ considerably. Further, some characters which vary on an age or a sex basis also vary geographically and within localities. Characters subject to such variation are: degree and extent of carapace granulation and hairiness, shape and orientation of anterolateral carapace teeth (especially with size), shape of anterior margin of front, relative carapace and chela proportions (the former with size, the latter with size and sex), hairiness of the male cheliped, degree of surface granulation of the male cheliped, size and shape of the teeth on the cutting margins of the male chela, extent of granulation and/or tuberculation of the pereopods, etc. Some characters are particularly variable in particular species, e.g. length of ocular peduncle and relative sizes of the anterolateral teeth in *M. telescopicus*, shape of the anterolateral teeth in *M. latreillei*, and carapace surface and pereopod granulation and tuberculation in *Venitus*.

What then remains for use as specifically diagnostic characters? Many of the variable characters briefly outlined above vary within fairly well defined limits and usually such characters can be utilized (with caution) if only adult males are made the basis of the classification. In *Macrophthalmus* (*sensu stricto*) and *Mareotis*, which contain between them some seventy percent of the probably valid living species of this genus, closely related species (i.e. those sharing a very similar morphological facies) without exception show constant differences of type or range in various features of their male chelipeds. These differences include the presence or absence of a large tubercle on the inner surface of the palm (in *Macrophthalmus*); the presence, number, or absence of spines on the inner surface of the carpus; the granulation

and tuberculation on the various surfaces and margins of the merus and index ; the size, number and distribution of granules on the outer surface of the palm ; the degree of deflexion of the index ; the presence or absence of differentiated teeth on either finger ; and (with caution) the distribution of hair on the cheliped ; in addition to the relative lengths and heights of the constituent segments. Other distinguishing features can be noted from the preceding systematic account. The other subgenera show similar differing characteristics, but as they contain few species each, the problem is not nearly so acute.

The features by which the various species differ and which are subject to least variation are then those manifested by the male chelipeds, whilst the females and juveniles of some species can only be identified with difficulty and uncertainty. It is tempting to draw parallels between this genus and other ocypodids, such as *Uca*, in which much of the taxonomy is based on the detailed structure of the male chelae. The latter appendages are used in behavioural exchanges intraspecifically and may function as specific isolating mechanisms. Few *Macrophthalmus* species have had their intraspecifically oriented behaviour investigated and therefore too many parallels cannot legitimately be drawn. But as no other functional significance for the different variations on a granular theme is apparent, either this or "side effects" of predominantly behavioural or physiological genes remain the most probable explanations of these specific distinguishing characters.

TAXONOMIC CONCLUSIONS

1. *M. sulcatus*, *M. sandakani* and *M. malaccensis* are synonymous and together form a southern and western subspecies of *M. dilatatus*, *M. dilatatus sulcatus*. Lanchester's (1900b) record of *M. carinimanus* is also of this subspecies. *M. dilatatus* (*sensu de Haan*), "*M. malaccensis*" and "*M. sulcatus*" form a series, progressing from north east to south west, along which clinal changes in a number of characters can be discerned.

2. *M. erato* is a primitive member of the subgenus *Mareotis*, and not *Mopsocarcinus* as earlier suggested (Barnes, 1967). It is evidently closely related to *M. crinitus*.

3. The following changes in synonymy are necessary, as the records were based on misidentifications :

Species recorded	Author	Identity of record
<i>M. convexus</i> ("abberant male")	Kemp, 1919	<i>M. parvimanus</i>
<i>M. consobrinus</i>	Crosnier, 1965	<i>M. parvimanus</i>
<i>M. depressus</i>	Lanchester, 1900b	<i>M. pacificus</i>
<i>M. teschi</i>	Gordon, 1931	<i>M. definitus</i>
<i>M. quadratus</i>	McNeill, 1968	<i>M. bosci</i>

4. *M. convexus kempi* Gravely is synonymous with *M. parvimanus*, a species very closely related to *M. convexus*.

5. *M. malayensis* Tweedie is synonymous with *M. laevimanus* H. M. Edwards.

6. The status of *M. brevis* (= *M. carinimanus*) cannot be fully unravelled at the present time. Lanchester's (1900a) record of *M. crassipes* is not of that species, but may provisionally be grouped with *M. brevis*, although the material is best regarded as *incertae sedis*, together with *M. dilatatus carens* Lanchester, 1900, pending a revision of *M. brevis*.

7. *M. hirtipes* has converged with sesarmine grapsids of the genera *Metaplex* and *Helice* in the structure of a number of carapace features mainly associated with burrowing and reoxygenation of the water in the branchial cavities.

ACKNOWLEDGEMENTS

The author is indebted to the Director and the Trustees of the British Museum for allowing the examination of material in their care, to Dr. A. L. Rice and Dr. R. W. Ingle for their help during this study, and to Dr. W. Macnae and Dr. J. D. Taylor for the Aldabra material in their charge.

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Printed in Great Britain by
Alden & Mowbray Ltd
at the Alden Press, Oxford

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SYSTEMATICS OF NEMATODES
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SYPHACIA SEURAT, 1916



C. G. OGDEN

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ZOOLOGY

Vol. 20 No. 8

LONDON : 1971

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 ref

Pp. 253-280 ; 5 Plates, 39 Text-figures

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THE BULLETIN OF THE BRITISH MUSEUM
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Bull. Br. Mus. nat. Hist. (Zool.).*

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TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 8 February, 1971

Price £1.20

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By COLIN G. OGDEN



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SUMMARY

The genus *Syphacia* is reviewed and its subgeneric division suggested by Chabaud and Biocca (1955) is discussed. Methods for preparing fresh and preserved specimens for examination by the scanning electron microscope are compared. It is suggested that the structure of the head in *Syphacia* falls into four distinct patterns, and it would appear that this feature may be of value, as in other oxyurids, for delimiting groups of species. The structure of the head, cuticle and the male mamelon as seen by the scanning electron microscope are illustrated. The use of measurements for comparative studies in parasitic nematodes is discussed. Four species: *S. obvelata*, *S. emilromani*, *S. stroma* and *S. muris* are compared and the methods for expressing this data are reported. Eleven species of the genus are redescribed, and it is confirmed that *S. obvelata* and *S. stroma* are distinct species.

INTRODUCTION

MANY of the descriptions of nematodes belonging to the genus *Syphacia* Seurat, 1916, appear to be inadequate by modern standards, with the result that difficulty may be

encountered in recognizing species which have been attributed to it. The writer became very aware of this difficulty when attempting specifically to determine some specimens of this genus recovered from the large intestine of the Lesser Bandicoot Rat, *Bandicota bengalensis*, in India. Owing to the abundance of both sexes in this material, the opportunity has been taken to study the morphological features found in these specimens and to compare them with similar features in specimens of *Syphacia* from various hosts already in the collections of the British Museum (Natural History). Use has also been made of the "Stereoscan" scanning electron microscope to elucidate certain structures which, although seen with the light microscope, are more accurately represented by the former instrument.

THE GENUS *SYPHACIA*

The genus *Syphacia* was erected by Seurat (1916) to accommodate two species formerly associated with the genus *Oxyuris*, namely, *O. obvelata* (Rudolphi, 1802) and *O. pallaryi* Seurat, 1915.

Tiner (1948) in his review of the genus listed thirteen species, and suggested that *S. stossichi* (Setti, 1897) and *S. trichosuri* Johnston & Mawson, 1938, should be treated as *Oxyuris* (*sensu lato*) species. This treatment of these species has been accepted by Chabaud & Biocca (1955) and Skrjabin et al. (1960). One of the species listed by Tiner, namely, *S. obubra* Baylis, 1936, has since been designated as the type-species of the genus *Syphaciurus* Skrjabin & Schikhobalova, 1951. This opinion is based mainly on the unusual structure of the head of the female specimens and has been accepted by Chabaud & Biocca (1955), Yamaguti (1961) and Chabaud (1965). Khera modifies Tiner's (1948) differential key slightly and adds another species, *S. tineri* Khera, 1956.

Nineteen species of *Syphacia* are listed and described by Skrjabin, Schikhobalova and Lagodovskaya (1960), one of which, *S. montana* Yamaguti, 1943, was apparently overlooked by Tiner (1948), Chabaud & Biocca (1955) and Khera (1956) in their lists of species. Some comparative studies have been made by Kruidenier, Mehra & Harkema (1961) on the differences between *S. peromysci* and *S. samorodini*, previously considered to be synonymous by reviewing authors, however, they suggest that it would be better at present to regard both species as distinct.

Division into subgenera

Chabaud & Biocca (1955) have used the number of mamelons in the males for dividing the genus into two subgenera, namely (*Syphacia*) possessing three mamelons and (*Syphatineria*) possessing two mamelons. The subgenus (*Syphacia*) automatically has *S. obvelata* as its type-species and these authors include ten other species :—*S. arctica* Tiner & Rausch, 1950 ; *S. baylisi* ; *S. frederici* ; *S. muris* ; *S. nigeriana* Baylis, 1928 ; *S. peromysci* Harkema, 1936 ; *S. ratti* ; *S. stroma* ; *S. thompsoni* Price, 1928 and *S. venteli*. According to Chabaud & Biocca the second subgenus (*Syphatineria*) has *S. pallaryi* as its type-species, and includes six other species :—*S. citelli* Tiner & Rausch, 1950 ; *S. eutamii* Tiner, 1948 ; *S. paraxeri* Sandground, 1933 ; *S. pearsei* Baylis, 1928 ; *S. sciuri* Mirza & Singh, 1934 and *S. transafricana* Chabaud & Biocca, 1955. The total number of species attributed to the

genus by Chabaud and Biocca is therefore eighteen. They also observed that the species appear to be divided on the basis of the family to which the host belonged in the Order Rodentia. Those species with hosts attributed to murine rodents being in the subgenus (*Syphacia*), whilst those with hosts in sciurine rodents being in the subgenus (*Syphatineria*).

The division of *Syphacia* into two subgenera is accepted by Skrjabin, Schikhobalova & Lagodoskaya (1960), who list three additional species, *S. lahorea* Akhtar, 1955; *S. tineri* Khera, 1954 and *S. montana* Yamaguti, 1943, belonging to the subgenus (*Syphacia*). The Russian authors' classification seems to disregard Chabaud & Biocca's subgeneric division on biological grounds, because *S. (Syphacia) lahorea* occurs in a sciurid in addition to the transference of *S. sciuri* to (*Syphacia*).

Recently, twelve additional species have been ascribed to the genus, namely: *S. (Syphacia) emilromani* Chabaud, Rausch & Desset, 1963; *S. srivastavi* Sinha, 1957; *S. (Syphatineria) tjanschani* Ablassov, 1962; *S. (Syphatineria) toschevi* Petrow & Bayanov, 1962; *S. (Syphacia) coli* Schmidt & Kuntz, 1968; *S. (Syphacia) magnispiculata* Schmidt & Kuntz, 1968; *S. (Syphacia) critesi* Schmidt & Kuntz, 1968; *S. (Syphatineria) oceanica* Schmidt & Kuntz, 1968; *S. (Syphacia) lophuromyos* Quentin, 1966; *S. (Syphacia) megaloon* Quentin, 1966 and *S. (Syphacia) alata* Quentin, 1968. Nevertheless, *S. srivastavi* must be treated as a doubtful species because it was described (Sinha, 1957 & 1960) from female specimens found in the stomach of the domestic pig, whereas the normal location of *Syphacia* species is the large intestine or caecum of rodents. The description and figures, particularly that of the head, do not appear to agree with the diagnosis of the genus *Syphacia*.

SCANNING ELECTRON MICROSCOPY

Live specimens of *Syphacia stroma* were collected from the intestine and caecum of *Apodemus flavicollis*, captured in the New Forest, Hampshire, England. Two methods of preparing these specimens for examination by the scanning electron microscope have been tried. In the first method the animals were washed several times with distilled water, then with a minimum of water they were frozen to -20°C , transferred to a freeze-drying unit and reduced to -50°C (Harris, 1968); in the second method they were fixed in 4% glutaraldehyde in 0.1 M cacodylic acid buffer, washed several times in the buffer followed by several washes in distilled water and freeze-dried as above. This latter method appears to produce the best results, because the body-cuticle is clean, whereas with the first method the body-cuticle is overlaid with mucus.

Preserved specimens of all the species dealt with in this report, with the exception of *S. pearsei*, have been examined, although in five cases it has only been possible to examine female specimens. The preserved specimens are transferred from either 4% formalin or 80% alcohol in a series of gradual dilutions to distilled water. It appears from specimens examined that formalin fixation is preferable to alcohol fixation. Unfortunately, the original fixative used in all cases is unknown and no conclusive result can be drawn in this instance. The distilled water used in all the methods outlined above is triple-glass distilled.

The reason for using the scanning electron microscope in the examination of these

species is that it is often difficult to interpret light-microscope studies of *en face* preparations and adequately to present the results. This microscope has assisted in both these respects, as it is now possible to examine whole specimens to a higher magnification and to illustrate them. The main difficulty encountered in the examination of *en face* features with the present material is that the lip-structure of those preserved specimens having large lip lobes has collapsed or distorted on freeze-drying, as a consequence the *en face* micrographs of *S. obvelata* and *S. muris* are not included in this report. The structure of the cuticle is not discussed in detail, because of the uncertainty of interpreting the structures seen. Nevertheless, it would appear that in some species the cuticle is smooth, whilst in others there are small longitudinal ridges additional to the normal transverse striations (compare Pl. 5, figs. A & C). On the cuticle of female specimens of one species, *S. transafricana*, bacteria are seen lying in the transverse ridges (Pl. 5, fig. C). An additional feature of the male mamelons of the five species examined is the presence of small papilla-like structures, which appear to be arranged in lines between the annulations. Examination of the cloacal region of male specimens in the present material has not been successful.

GENERAL MORPHOLOGY

The cuticle is marked with distinct transverse striations. Narrow lateral alae commence at the anterior end of the body and terminate slightly anterior to the level of the anus ; they are present in both sexes. The cuticle in the cephalic region is often inflated to form a cephalic vesicle, and cervical alae are sometimes present.

The oesophagus is characterised by a small, unmodified pharyngeal portion, followed by the usual club-like corpus which is constricted prior to the oesophageal bulb. The triradiate valvular apparatus of the posterior bulb is typical of oxyurids. The anterior half of the oesophagus is modified by the folding of the oesophastome, to give the appearance of tooth-like structures. These structures are described by Yamaguti (1943) as a specific character of *S. montana*. Nevertheless, this feature is present in all of the specimens examined.

The nerve ring is situated approximately at the middle of the oesophagus. Ramisz (1965) has described the nervous system of *S. obvelata*. The excretory pore is usually found posterior to the oesophageal bulb, but anterior to the vulva in the female. Both of these characters are sometimes difficult to find. The tail in both sexes narrows to a sharp point.

Male. The posterior end of the body is usually curved ventrally. The cuticle is characterised by the presence of two or three bosses with distinct transverse ridges, referred to as mamelons, situated on the ventral surface, approximately between the middle of the body and the cloacal opening. Each ridge on the mamelons is split along its transverse axis into two shallow elevations, between which lie small papilla-like structures (Pl. 4, fig. D). There is no distinct pattern in the distribution of the mamelons on the body, although they give the appearance of being equally spaced, this, however, is not the case. The size and structure of the mamelons appears to depend to a large extent on the age of the specimen and the degree of ventral curving to the posterior end of the body, the latter feature causes the annules of the cuticle

to become compacted and the mamelon to protrude from the normal body line. This is easily seen in specimens recovered in sufficient numbers from one host, where the variation of ventral curving can range from only slight to perhaps two complete coils. The mamelons are usually recognizable macroscopically, but occasionally it is necessary to examine the specimens ventrally to see the most anterior mamelon. The cuticle around the cloacal opening is inflated slightly to form small caudal or bursal alae which extend from the most anterior pair of pre-cloacal papillae to the post-cloacal papillae. There are three pairs of caudal papillae, a medium-sized pair just anterior to the cloacal opening, a smaller pair level with the cloacal opening and a large pair posterior to the cloacal opening. There is a single spicule, which is pointed distally, and a complex gubernaculum.

Female. The vulva is situated in the anterior third of the body, behind the level of the oesophageal bulb. It is slightly protruded in some specimens and occasionally has a dark brown cap covering the tip (Pl. 3, fig. F). The vagina is short and the musculature of the ovijector is well developed. The uterus is single, usually filling the body-cavity posteriorly and sometimes extending anteriorly beyond the vulva. The eggs are usually flat on one side and smoothly curved on the other.

Structure of the head

The following features are common to all the species studied. The mouth opening is small and circular, leading into a shallow buccal cavity. The head bears three lips of equal size, two sub-ventral and one dorsal, with the cephalic papillae and amphids situated slightly posterior to them. The four single cephalic papillae are dorso-and ventrolateral in position, whilst the lateral amphids are slightly anterior to their level. In addition, an inner circle of six circumoral papillae is present in some species (see fig. 4).

There appear to be four distinct patterns in the form of the head. The first is represented in three species, *S. citelli*, *S. pallaryi* and *S. transafricana*, in which the lips are reduced in size (fig. 6) and have a cuticular thickening giving them a distinct triangular shape (Pl. 2, fig. B). The second is found in five species, *S. obvelata*, *S. emilromani*, *S. stroma*, *S. peromysci* and *S. muris*, all having pronounced lip-lobes (fig. 5, Pl. 1, figs. A & C) and occasionally an inner thickening of the cuticle to form a toothlike structure. The third is found in only two species, *S. pearsei* and *S. thompsoni*, in which the lip-lobes are separated from each other. The space between the lips extends to form interlabial grooves (fig. 7, Pl. 1, fig. E), which are similar to those described as either "labial grooves" in some Ascarid species or "cervical cordons" in the Heterakidae. The fourth pattern is represented only in *S. eutamii*. In this species the lips are supported by individual cuticular processes from the buccal cavity, with a supporting septum connecting it to the apical region of each lip (Pl. 3, fig. B). Individual variations of these four patterns are reported later under the species description.

COMPARATIVE MEASUREMENTS

The presentation of measurements in comparing species of this genus can be misleading, because of the similarity in the overall size of these animals. For example,

there are eight species with three mamelons in which the body-size of the male lies between one and two millimetres. The usual methods of presenting measurements of nematodes are confined to four approaches ; ratios ; graphically ; individual animal measurements ; and the mean value of a series of measurements.

If the ratios normally used in describing free-living nematodes are applied to

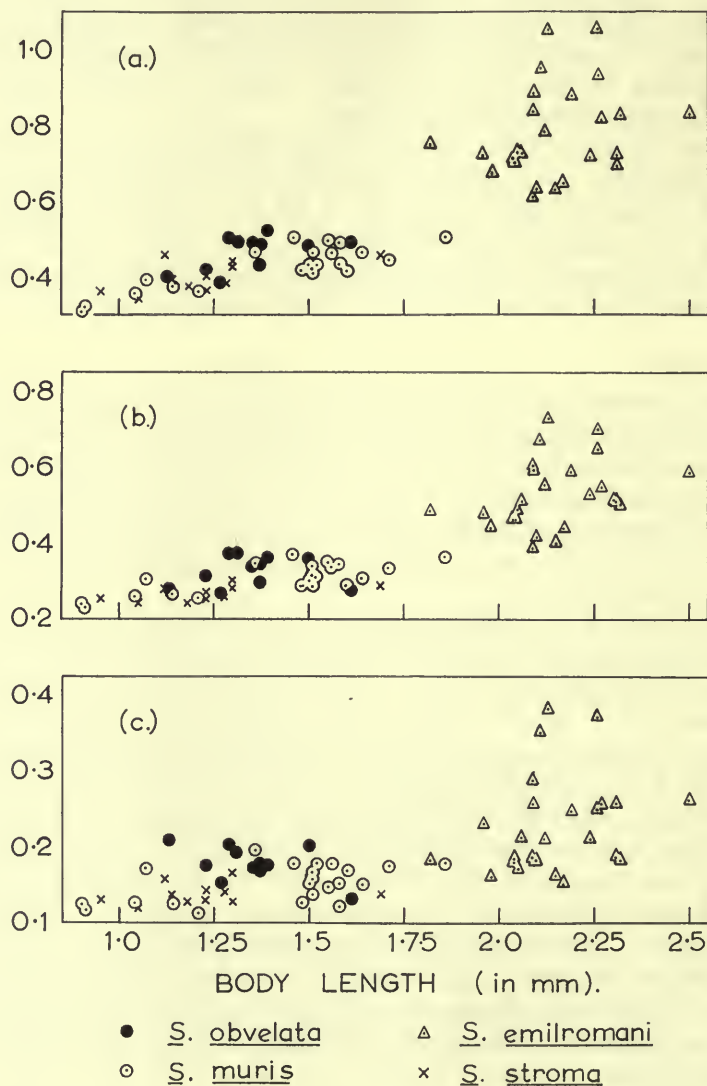


FIG. 1. Distance of mamelons from cloacal opening of male, vertical scale ; plotted against the total body length, horizontal scale (all measurements in mm) : (a) anterior mamelon (b) middle mamelon (c) posterior mamelon.

parasitic nematodes the limitation of each species will depend on the number of specimens found infesting the host-animal, or in a series of similar hosts collected in the same locality at the same time. That preservation can have a marked effect on such ratios has been pointed out by Inglis (1957), who considers that "V" appears to be the ratio least likely to show the effects of preservation, agreeing in part with Taylor & Jenkins (1957). In summarising the use of these ratios, with reference to their use in comparing parasitic nematodes, Inglis concludes that ratio "a" is unreliable. Regarding ratio "c", he considers that it may be particularly sensitive to variation in the length of the body when the tail of a species is narrow and in the form of a cuticular spike.

Only Roman (1951), of those authors who have used measurements for comparative purposes in the genus *Syphacia*, has used a graphical approach by means of "polygones de frequence". Some authors have listed individual measurements, but most have restricted their observations to listing only the range and mean of each of the characters used. For example, Hussey (1957), Kruidenier et al. (1961) and Bernard (1963) all give tables of measurements.

The species used in this present comparison of measurements, *S. obvelata*, *S. emilromani*, *S. stroma* and *S. muris* have been recovered from *Clethrionomys glareolus*, *Apodemus sylvaticus argenteus*, *Apodemus s. sylvaticus* and *Bandicota bengalensis*, respectively. The specimens of *S. obvelata*, eleven males to approximately one hundred and twenty females, are from the caecum of three hosts caught in Witham Woods, near Oxford. Those of *S. emilromani* are from the intestine of one host from North Honschu, Japan, and those of *S. stroma* are from one host from Bagley Wood, near Oxford, both of these infestations are large, but they are represented by a proportion of roughly 1 : 10 males to females. The specimens of *S. muris*, twenty-two males to approximately sixty females, are from the large intestine of two hosts, caught in Calcutta, India, and are unusual in the proportion of male to female specimens being small. All male specimens have been measured, with the exception of *S. emilromani*, where an arbitrary number of twenty-five has been taken. Further twenty-five female specimens taken at random from each species have also been measured.

The individual measurement for each character in this study has been taken at the same position, or as near as possible, in each specimen. The measurement for the male mamelon is the distance between the middle of each mamelon and the cloacal opening. In the male, the body-breadth has been taken at a point just anterior to the foremost mamelon, whereas in the female it has been taken just posterior to the vulva. A maximum of three eggs, selected at random, from each gravid female have been measured. The range of measurements for the species are given in Table 2, the figures in brackets being the mean values.

Using the mean values as a comparison of the measurements given in Table 2a, the values obtained from the males of *S. obvelata* and *S. stroma* appear to be in close agreement, while *S. emilromani* appears to be larger than these two species in all dimensions, except in the length of the spicule and the gubernaculum, and *S. muris* differs in the size of the spicule, gubernaculum and tail from the other three species. A similar comparison of the females, Table 2b, shows that *S. obvelata* appears to differ

in the length of the tail from the other three species and in the position of the vulva from *S. muris* and *S. emilromani*; *S. stroma* appears to have the smallest tail, but the position of the vulva is similar to *S. obvelata*; *S. emilromani* differs from the other species in the length of its oesophagus. In size, the eggs of *S. emilromani* and *S. muris*

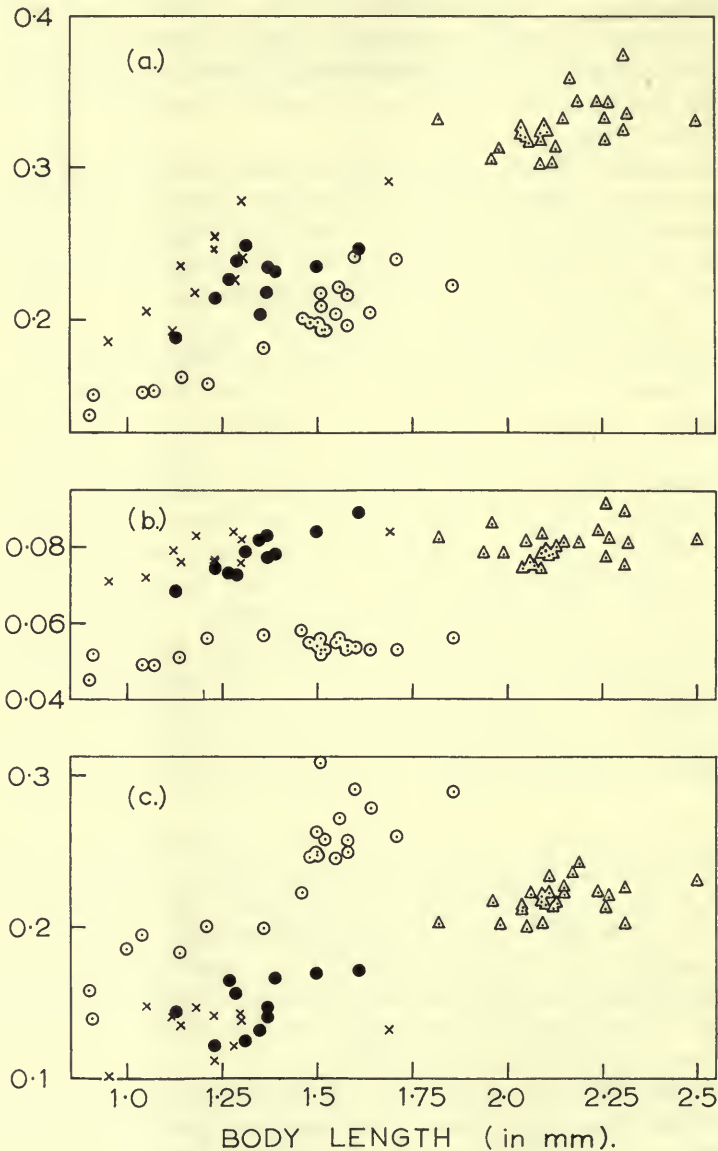


FIG. 2. Comparison of males : (a) length of oesophagus (b) length of spicule (c) length of tail, vertical scales; plotted against the total body length, horizontal scale (all measurements in mm). Symbols for each species are given in Fig. 1.

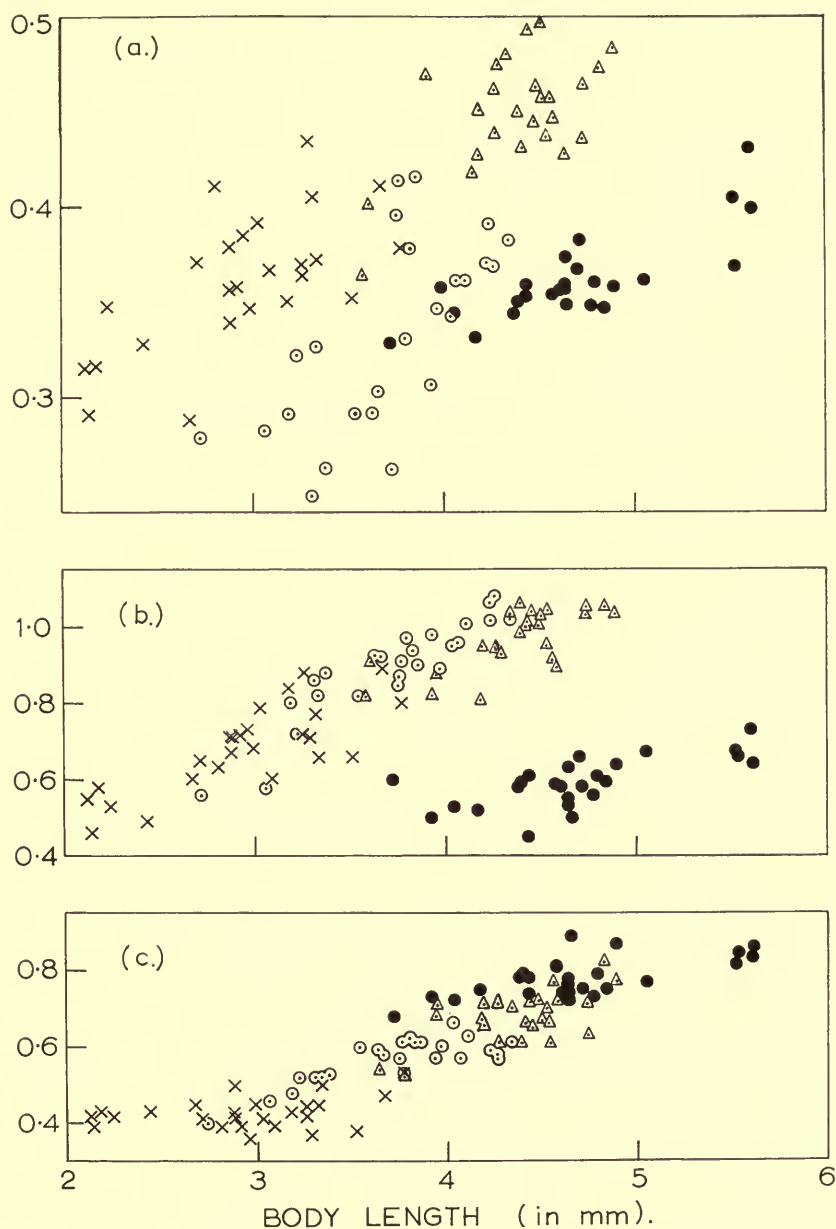


FIG. 3. Comparison of females : (a) length of oesophagus (b) distance of vulva from anterior end of body (c) length of tail, vertical scales ; plotted against the total body length, horizontal scale (all measurements in mm). Symbols for each species are given in Fig. 1.

are similar, but differ from those of *S. obvelata* and *S. stroma*, the latter, the smallest species, having the largest eggs.

By expressing these results graphically it is possible to examine the distribution of the individual measurements. To determine the value of the position of the mamelons on the males as a specific character, the distance of each mamelon from the cloacal opening is plotted against the body-length (fig. 1). The distance from the cloacal opening being used in preference to the distance from the posterior end of the body, in an attempt to eliminate any variation due to the species in the length of the tail. It is evident from the scatter of this data that the position of these structures is not suitable for use as a specific character, in fact the scatter might suggest that the structures are uniformly distributed.

It appears (fig. 2) that the correct assumptions have been assessed from the tables of measurements of male specimens, *S. muris* being distinct in the size of the spicule and tail. The size of the spicule is plotted (fig. 2 (b)) to show that there is no apparent effect of body size on this feature. The females (fig. 3), appear to fall into two groups on the basis of the length of the oesophagus, *S. stroma* and *S. emilromani* having the longer, with *S. muris* and *S. obvelata* the shorter oesophagus. Only *S. obvelata* differs from the others in the position of the vulva, and there is no apparent difference between any of the species in the length of the tail. These results are in some ways contrary to the conclusions drawn from the tables of measurements discussed above.

The results expressed as ratios, together with the standard deviation and range of values are shown in Table I. Considering the males first, there appear to be differences in ratio "b" between all four species. The difference in ratio "c" between *S. muris* and the other species is considered to be distinct. The female specimens appear to fall into two groups using ratio "b": (i) *S. obvelata* and *S. muris*; and (ii) *S. emilromani* and *S. stroma*. Ratio "c" appears to be similar for all four species, although the variation exhibited in the range of values for *S. stroma* cannot be explained. The difference in ratio "V", shows that *S. obvelata* can easily be differentiated from the other three species.

To summarise the results of the present comparison of measurements: the males of *S. muris* can be differentiated from the other three species by the size of the spicule, gubernaculum and tail; the males of *S. emilromani* are larger in body-length than the other three species, but there is no apparent difference between *S. obvelata* and *S. stroma*; the females of *S. obvelata* are distinct in the position of the vulva, and those of *S. stroma* in the size of the eggs; it also appears that the females of *S. obvelata* and *S. muris* differ in the size of the oesophagus from *S. stroma* and *S. emilromani*.

The conclusions that can be drawn from the methods used are that expressing the results as mean values is unsatisfactory for comparative purposes and preference must be given to the use of graphs or ratios. This is certainly the case when the infestation contains numerous specimens. In those instances where the infestation is numerically poor, it seems imperative to quote individual measurements to enable future comparisons of this nature to be made.

DESCRIPTION OF SPECIES

Syphacia obvelata (Rudolphi, 1802)

S. artica Tiner & Rausch, 1950

S. montana Yamaguti, 1943

S. nigeriana Baylis, 1928

MATERIAL STUDIED. 11 ♂♂, 25 ♀♀ ex caecum *Clethrionomys glareolus*. Witham Wood, Oxford. B.M. (N.H.) Reg. Nos. 1966.329-378.

1 ♂, 5 ♀♀ ex intestine *Microtus agrestis neglectus*. Loch Tay, Perthshire. B.M. (N.H.) Reg. Nos. 1964.1697-1715.

5 ♂♂, 25 ♀♀ ex *Clethrionomys rufocanus bedfordiae*. Rebun Island, Hokkaido, Japan.

3 ♂♂, 10 ♀♀ ex intestine *Taterillus gracilis angelus*, *Taterona kempi*, *Praomys tullbergi*, *Mastomys erythroleucus* and (?) *Lemniscomys striatus*. Nigeria. Co-types & Paratypes of *S. nigeriana*. B.M. (N.H.) Reg. Nos. 1929.1.24.25-44.

2 ♂♂, 5 ♀♀ ex hind-gut *Mus dubius*. Colombo, Ceylon. B.M. (N.H.) Reg. Nos. 1935.9.12.51-75.

1 ♂, 5 ♀♀ ex caecum 'water-voles'. Salop, Perthshire. B.M. (N.H.) Reg. Nos. 1935.6.4.142-153.

MEASUREMENTS (in mm) See Table 2.

The cuticle is transversely striated and has small longitudinal ridges, similar to those occurring in *S. eutamii* (see Pl. 5, fig. A). The anterior end of the body has small cervical alae, which arise anteriorly and terminate at approximately the level of the oesophageal bulb. The head bears three prominent lip-lobes (fig. 5).

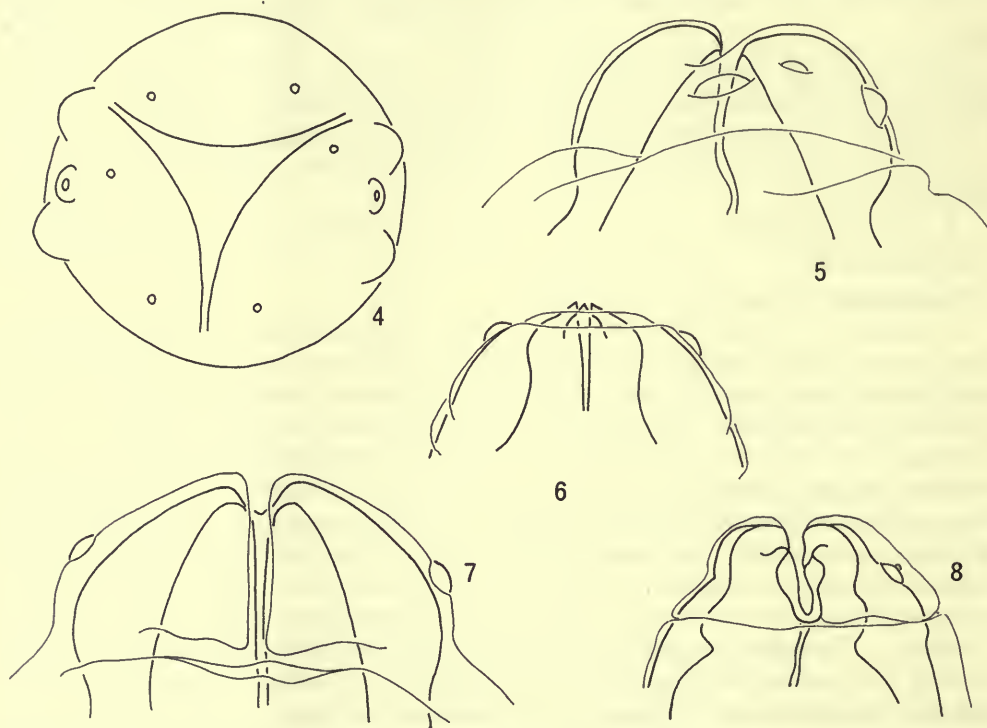
Male. The three mamelons have six or seven small papilla-like structures lying between their striations (Pl. 4, fig. D); the pre-cloacal and smaller cloacal papillae lie close together, whilst the post-cloacal pair are pronounced (figs. 9 & 13); the single spicule narrows slightly at approximately one-third of its total length from the proximal end and terminates distally in a sharp point (figs. 23 & Pl. 3, fig. E); the gubernaculum is complex (fig. 15); the tail tapers evenly to a fine point.

Female. The vagina normally runs posteriorly, but in some specimens, in which the uteri are packed with eggs, it is bent anteriorly; the lips of the vulva are protruded in some specimens; the eggs are of medium size (fig. 19 and Table 2b).

DISCUSSION. It is impossible to recognise *S. obvelata* from its original description (Rudolphi, 1802) based on specimens from *Mus musculus*, or from the later description (Rudolphi, 1809) which was based on material from two hosts. This species has since been described by numerous authors, but the available information is still insufficient to differentiate it from other members of the genus, so that, two species, namely *S. obvelata* and *S. stroma*, have been reported to occur in the same host. It is now generally accepted, however, that *S. obvelata* is parasitic in the house-mouse, the bank-vole and the field-vole, whilst *S. stroma* is parasitic in the field mouse. Unfortunately, the collections of the British Museum (Natural History) have male specimens only from voles, but these appear to be sufficiently different from those from field-mice to enable them to be accepted as being specimens of *S. obvelata*.

The uncertainty of the specific characters of *S. obvelata* has led to the description

of several new species with slightly differing characters. The validity of these species is therefore difficult to determine, unless a direct comparison with specimens of *S. obvelata* is undertaken at the same time. None of the authors seem to have done this, although they all compare their species with descriptions of *S. obvelata*. For example, Yamaguti (1943) describes *S. montana* as differing from *S. obvelata* in the length of the oesophagus and the accessory piece (= gubernaculum). Similarly, Baylis (1928) differentiates *S. nigeriana* from *S. obvelata* thus "... notably in the much greater length of the tail in the female, and in other minor points", whilst Tiner & Rausch (1950) could not differentiate the males of *S. obvelata*, *S. nigeriana*,



FIGS. 4-8. 4. *En face* view of head, *S. stroma*. 5. Dorsal view of head, *S. obvelata*. 6. Dorsal view of head, *S. pallaryi*. 7. Dorso-lateral view of head, *S. thompsoni*. 8. Dorso-lateral view of head, *S. pearsei*.

S. venteli and *S. muris* from their species, *S. arctica*, but considered the size of the eggs and the length of the female tail sufficiently different to warrant the erection of a new species.

A comparison of the measurements of specimens of *Syphacia* from *Clethrionomys glareolus* and *C. ruficanus*, the latter being the type-host of *S. montana* (see Chabaud et al. 1963), are shown in Tables 2 & 3. The agreement between the two sets of measurements is close. In addition, using the ratios: $b\ 6.38 \pm 0.81$; $c\ 8.79 \pm 0.73$ males and $b\ 12.63 \pm 0.95$; $c\ 5.60 \pm 0.34$; $V\ 14.7 \pm 1.44$ females, the comparison

with those for *S. obvelata* Table 1 is good. The morphological characters of the two sets of specimens are also closely comparable, and accordingly *S. montana* is here treated as a synonym of *S. obvelata*.

The length of the female tail does not appear to be a specific character in the group of species examined earlier in this report, and although the eggs of *S. arctica* are slightly smaller than any the writer has seen in *S. obvelata* it is not considered that this character alone is sufficient to warrant a separate species. It is therefore suggested that *S. arctica* be treated as a synonym of *S. obvelata*.

The type-specimens of *S. nigeriana* have been re-examined, and they appear to be conspecific with *S. obvelata*. This is in agreement with the observation made by Bernard (1963) from a study of *Syphacia* specimens from *Gerbillus campestris* and *Mus musculus* in Algiers.

S. obvelata appears to be distinct principally in the structure of the head : in the male, the size and shape of the spicule and gubernaculum, in the pronounced post-cloacal papillae, in the length of the tail and the number and form of the mamelons ; in the female, the length of the oesophagus, in the position of the vulva and in the size of the eggs.

Syphacia emilromani Chabaud, Rausch & Desset, 1963

MATERIAL STUDIED. 25 ♂♂, 25 ♀♀ ex *Apodemus sylvaticus argenteus*. Mt. Hakkoda, North Honschu, Japan. Paratype specimens.

MEASUREMENTS (in mm) See Table 2.

The head bears three prominent lip-lobes (Pl. 3, figs. C & D).

Male. There are three mamelons on the ventral surface of the cuticle ; the pre-cloacal and cloacal papillae lie close together and the postcloacal pair are not pronounced ; the spicule (fig. 24) is similar to those of *S. obvelata* and *S. stroma* ; the gubernaculum is also similar in general appearance to that of *S. obvelata*, but differs in having a series of notches on the distal barb-like structure (fig. 16) ; the tail tapers evenly to a point.

Female. The vagina runs posteriorly from the vulva in all the specimens examined ; the eggs are small (fig. 20).

DISCUSSION. This species is considered by Chabaud et al. (1963)* to differ from the known species of the genus in the absence of oesophageal "teeth", in the position of the four cephalic papillae and the size of the eggs.

S. emilromani appears to be similar to *S. stroma* in many characters, including the structure of the head, but differs from it in the size of the body, the shape of the gubernaculum and the size of the eggs. It is also similar to *S. peromysci* and *S. samorodini* in the shape of the gubernaculum and in the size of the eggs. These species are, however, much smaller than *S. emilromani*.

S. emilromani is distinct in the structure of the head and in the size of the body: the male in the number of mamelons, in the small post-cloacal papillae, in the shape

* Note that in this (1963) description there is a typographical error, the length of the spicule being given as 195 μ instead of 95 μ .

of the gubernaculum and in the length of the tail ; the female in the length of the oesophagus, in the position of the vulva and in the size of the eggs.

Symphacia stroma (Linstow, 1884)

Oxyuris stroma Linstow, 1884

MATERIAL STUDIED. 11 ♂♂, 25 ♀♀ ex intestine *Apodemus sylvaticus*. Bagley Wood, Oxford. B.M. (N.H.) Reg. Nos. 1926.4.20.126-145.

3 ♂♂, 4 ♀♀ (immature) ex intestine *Apodemus sylvaticus*. Selsdon Woods, Surrey. B.M. (N.H.) Reg. Nos. 1934.7.19.10-15.

5 ♂♂, 6 ♀♀ ex intestine *Apodemus sylvaticus*. Carmarthenshire. B. M. (N.H.) Reg. Nos. 1956.8.16.3-6.

8 ♂♂, 12 ♀♀ ex intestine *Apodemus flavicollis*. Brockenhurst, New Forest, Hampshire. B.M. (N.H.) Reg. Nos. 1970. 63-68.

5 ♂♂, 10 ♀♀ ex intestine *Apodemus sylvaticus*. New Forest, Hampshire. B.M. (N.H.) Reg. Nos. 1970. 55-62.

5 ♀♀ ex intestine *Apodemus sylvaticus*. Charrade, France. B.M. (N.H.) Reg. Nos. 1935.11.6.190-193.

5 ♀♀ ex *Apodemus hebridensis*. Isle of Lewis, Hebrides. B.M. (N.H.) Reg. Nos. 1934.4.24.49-55.

MEASUREMENTS (in mm) See Table 2.

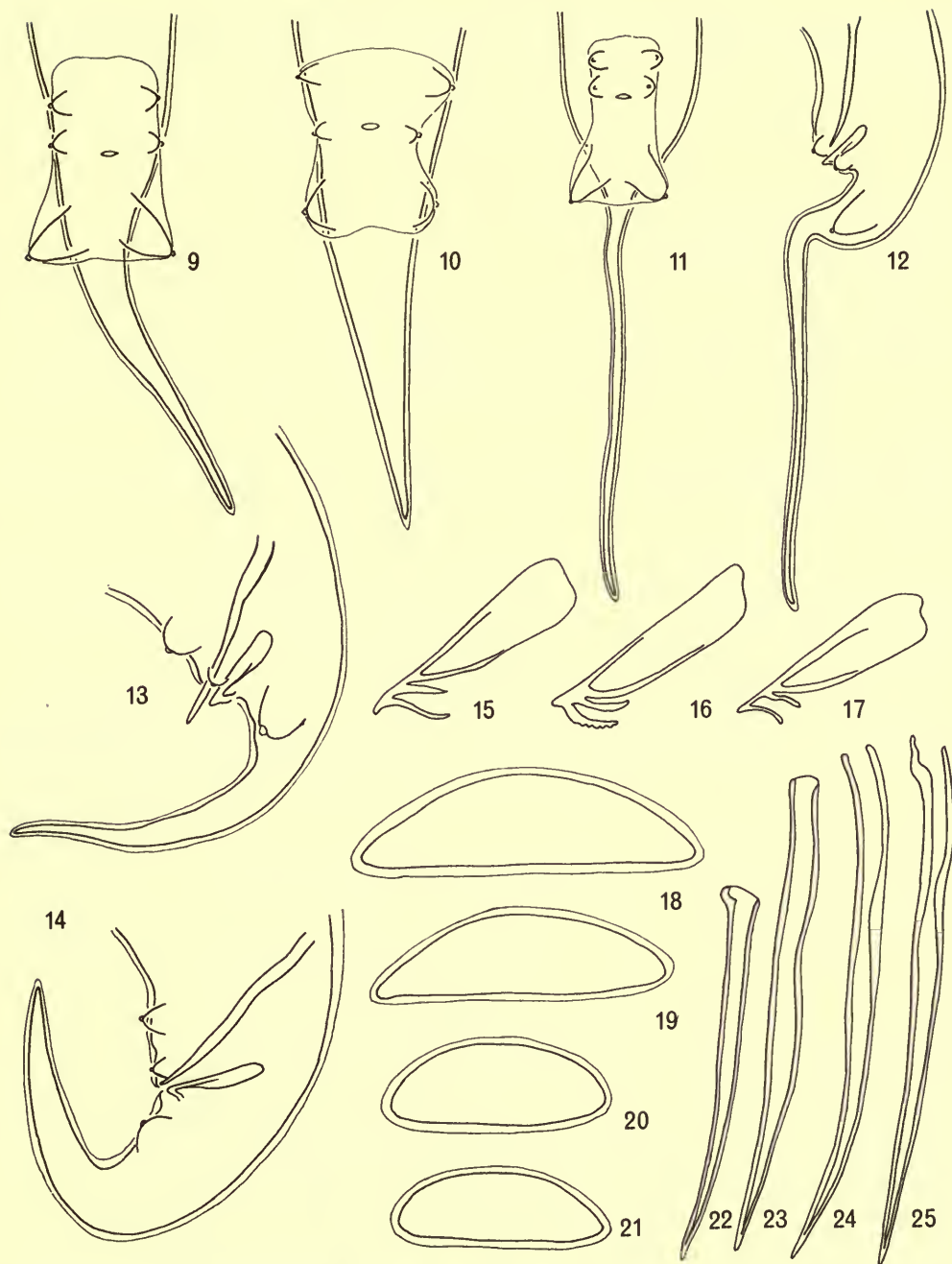
The head bears three prominent lip-lobes (Pl. 1, figs. A. B.). Cervical alae appear to be absent. An inner ring of six circumoral papillae is present (fig. 4).

Male. There are three mamelons ; between the transverse striations of each mamelon there are small papilla-like structures usually arranged in rows of five (Pl. 4, figs. B & E) ; the post-cloacal papillae are not pronounced (fig. 10 & 14) ; the spicule (fig. 25) and gubernaculum appear to be identical with those of *S. obvelata* ; and the tail tapers gradually to a fine point (fig. 10).

Female. The body-length in these specimens is the smallest of those examined, whereas the eggs are the largest (see Table 2b & fig. 18).

DISCUSSION. This species was first described by Linstow (1884), who considered that the female specimens differed from those of *S. obvelata* in the position of the vulva and in the size of the eggs. Later, Seurat (1915 & 1916) considered *S. stroma* to be a synonym of *S. obvelata*. Morgan (1932) showed that male specimens of these two species could be separated by the differences in the structure of the post-cloacal papillae and by the thickness of tail. Nevertheless, Baylis (1936) pointed out that difficulties still existed between these species, because Morgan (1932) did not compare female specimens. Roman (1951) describes this species and distinguishes it from *S. obvelata* in the length of the oesophagus, in the structure of the head and in the position of the mamelons. These authors, Linstow, Morgan and Roman, appear to be justified in some of these conclusions, but they individually failed to give a complete diagnosis of the specific characters.

Symphacia stroma is here considered to be distinct in the structure of the head ; the male in the number and structure of the mamelons, in the size of the post-cloacal



FIGS. 9-25. 9. Ventral view of male tail, *S. obvelata*. 10. Ventral view of male tail, *S. stroma*. 11. Ventral view of male tail, *S. muris*. 12. Lateral view of male tail, *S. muris*. 13. Lateral view of male tail, *S. obvelata*. 14. Lateral view of male tail, *S. stroma*. 15. Lateral view of gubernaculum, *S. obvelata*. 16. Lateral view of gubernaculum, *S. emilromani*. 17. Lateral view of gubernaculum, *S. muris*. 18. Egg of *S. stroma*. 19. Egg of *S. obvelata*. 20. Egg of *S. emilromani*. 21. Egg of *S. muris*. 22. Lateral view of spicule, *S. muris*. 23. Lateral view of spicule, *S. obvelata*. 24. Lateral view of spicule, *S. emilromani*. 25. Lateral view of spicule, *S. stroma*.

papillae and in the length of the tail ; the female in the length of the oesophagus, in the position of the vulva and in the size of the eggs.

Syphacia muris (Yamaguti, 1935)

Enterobius muris Yamaguti, 1935

Syphacia baylisi Maplestone & Bhaduri, 1942

Syphacia ratti Roman, 1945

Syphacia venteli Travassos, 1937

MATERIAL STUDIED. 22 ♂♂, 25 ♀♀ ex large intestine *Bandicota bengalensis*. Calcutta, India. B.M. (N.H.) Reg. Nos. 1966.213-252.

5 ♀♀ ex intestine of 'rats'. Pahang, Malaya. B.M. (N.H.) Reg. Nos. 1932.9.21. 1-4.

MEASUREMENTS (in mm) See Table 2.

The anterior region of the body bears small cervical alae. The head carries three lip-lobes.

Male. There are three mamelons ; the post-cloacal papillae are pronounced (fig. 11 & 12) ; the spicule is small and tapers to a fine point distally (fig. 22) ; the gubernaculum is small (fig. 17) ; and the tail tapers rapidly just posterior of the post-cloacal papillae and forms a long, thin terminal spike (fig. 11).

Female. The vagina is directed posteriorly and the eggs are small (fig. 21).

DISCUSSION. This species was initially described by Yamaguti (1935) as *Enterobius muris* from female specimens only, but later (1941) he redescribed it as *Syphacia muris* on examination of both male and female specimens. Baylis (1936) observed that specimens of *Syphacia* from *Rattus rattus* in India differed in the size and shape of the eggs from those of *S. obvelata* and *S. stroma*. He considered that this later character might prove to be a specific feature of these specimens. Subsequently, Maplestone & Bhaduri (1942) on examination of female specimens recovered from rats (*Mus decumanus* [= *Rattus norvegicus*]) in India, describe a new species, *S. baylisi*, using the size of the eggs to differentiate their species from *S. obvelata* and *S. stroma*. They also observe that "... these results confirm Baylis' opinion", suggesting that the two sets of specimens are conspecific.

Roman (1951) considers that *S. ratti*, which he described earlier (Roman, 1945), is on further examination a synonym of *S. baylisi*. He considers, however, that *S. baylisi* appears to be distinguishable from *S. muris* by the larger body-size and by the position of the vulva. Hussey (1957) compared specimens of *S. obvelata* and *S. muris* from experimental hosts and concluded that the two species are readily distinguishable. She agrees with Tiner (1948) that *S. venteli* and *S. muris* are synonymous.

A comparison of the descriptions and measurements given by Maplestone & Bhaduri (1942), Roman (1945 & 1951) for *S. baylisi* and by Travassos (1937) for *S. venteli*, with those given by Yamaguti (1935 & 1941) and the present material, shows that all these specimens agree in sufficient detail to warrant their reference to *S. muris*.

S. muris is distinct in the structure of the head : the male in the number of mamelons, in the pronounced post-cloacal papillae, in the size and shape of both the spicule and the gubernaculum, and in the length of the tail ; the female in the length of the oesophagus, in the position of the vulva and in the size of the eggs.

***Syphacia peromysci* Harkema, 1936**

MATERIAL STUDIED. 4♂♂, 7♀♀ ex *Peromyscus maniculatus*. Utah, U.S.A.

MEASUREMENTS. The material available is insufficient to contribute any significant information to that already available.

The head carries three pronounced lip-lobes (Pl. 1, figs. C & D).

Male. There are three ventral mamelons (Pl. 4, fig. A), each one having approximately five or six, small papilla-like structures lying in rows between the striations (Pl. 5, fig. D) and the structure of the gubernaculum is similar to that of *S. emilromani*.

DISCUSSION. Harkema (1936) separates this species from *S. obvelata* by its smaller size, by having projecting mamelons and by the size of the eggs. Kruidenier et al. (1961) consider it to be a valid species and distinguish it from *S. samorodini* by the possession of cervical papillae, by the position of the vulva, by the strength and position of the vagina and by the size of the eggs.

This species is similar to *S. samorodini* as shown by the comparative measurements of Kruidenier et al. (1961). Nevertheless, the difference in the position of the vulva may prove to be sufficient to separate *S. peromysci* and *S. samorodini* and both are here provisionally accepted as valid.

***Syphacia citelli* Tiner & Rausch, 1950**

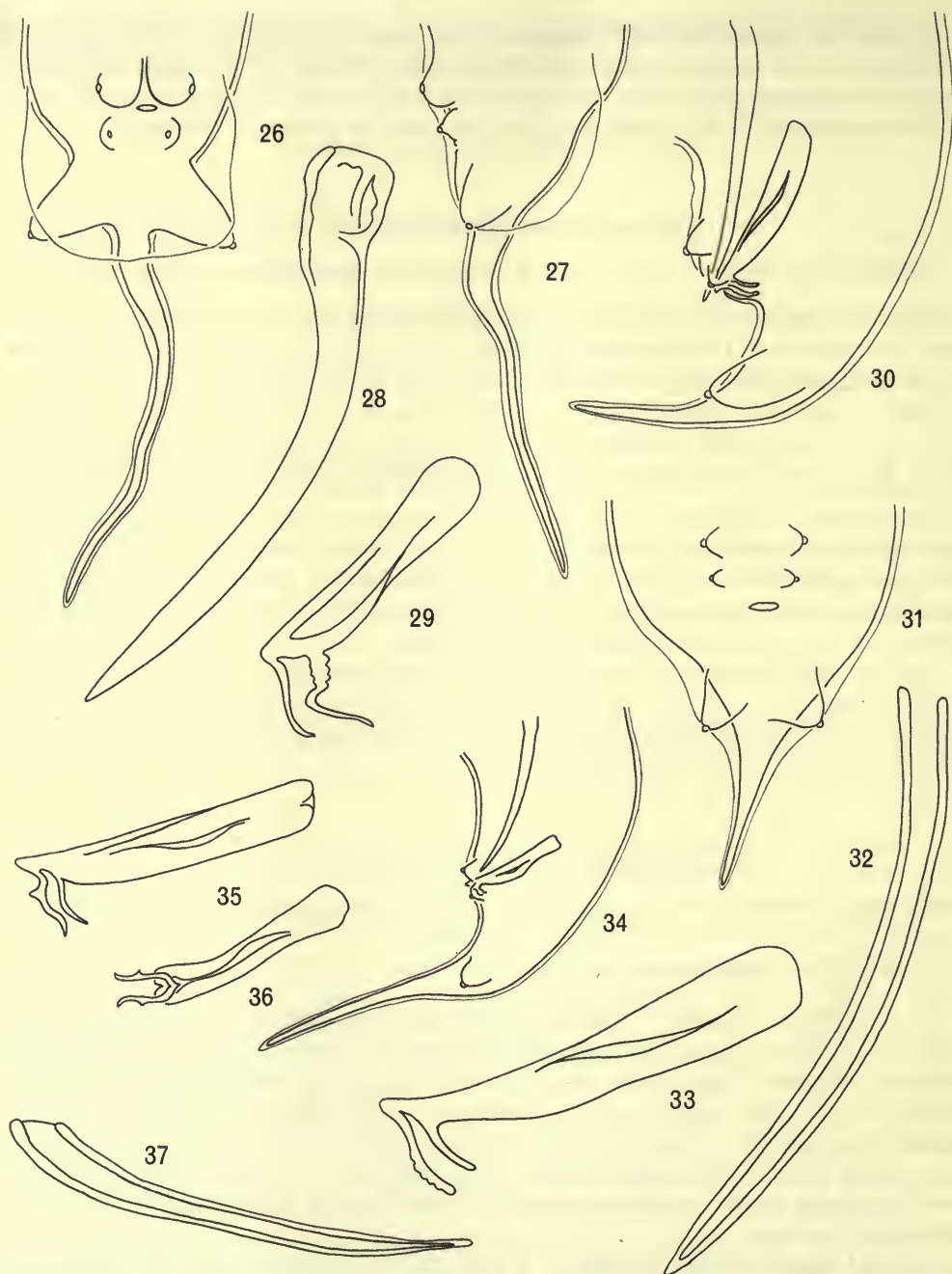
MATERIAL STUDIED. 6♂♂, 3♀♀ (juvenile) ex caecum *Citellus variegatus*. Utah, U.S.A.

2♂♂, 4♀♀ ex *Citellus variegatus*, Utah, U.S.A.

MEASUREMENTS (in mm). Males (from the first listed material only) : body-length 2.81, 2.82, 2.89, 3.01, 3.12, 3.16 ; body-breath 0.236, 0.252, 0.247, 0.272, 0.327, 0.398 ; diameter of head 0.043, 0.034, 0.045, 0.047, 0.044, 0.047 ; oesophagus length 0.408, 0.445, 0.434, 0.508, 0.477, 0.437 ; distance of mamelons from cloacal opening,—posterior 0.78, 0.69, 0.83, 0.87, 0.82, 0.79 ; —anterior 1.18, 1.18, 1.37, 1.62, 1.20, 1.13 ; length of spicule 0.092, 0.101, 0.100, 0.098, 0.104, 0.090 ; length of gubernaculum 0.025, 0.028, 0.029, 0.030, 0.032, 0.029 ; length of tail 0.189, 0.198, 0.191, 0.212, 0.177, 0.199.

Cervical alae appear to be absent. The head is not pronounced, and the lips appear to have a cuticular thickening (Pl. 2, fig. A). An inner circle of six circumoral papillae is present.

Male. There are two mamelons ; the small papilla-like structures seem to be arranged in rows of seven or eight between the transverse striations of the mamelons



FIGS. 26-37. 26. Ventral view of male tail, *S. citelli*. 27. Lateral view of male tail, *S. citelli*. 28. Lateral view of spicule, *S. citelli*. 29. Lateral view of gubernaculum, *S. citelli*. 30. Lateral view of male tail, *S. pallaryi*. 31. Ventral view of male tail, *S. pallaryi*. 32. Lateral view of spicule, *S. pallaryi*. 33. Lateral view of gubernaculum, *S. pallaryi*. 34. Lateral view of male tail, *S. transafricana*. 35. Lateral view of gubernaculum, *S. transafricana*. 36. Ventral view of gubernaculum, *S. transafricana*. 37. Lateral view of spicule, *S. transafricana*.

(Pl. 5, fig. B) ; the post-cloacal papillae are pronounced (figs. 26 & 27) ; the spicule is curved distally (fig. 28) ; the gubernaculum is complex (fig. 29) ; the tail tapers rapidly posterior to the post-cloacal papillae to form a long, thin, terminal spike (fig. 26).

Female. Although these specimens are almost ten times longer than those of *S. obvelata* the eggs are of a similar size; the tail tapers gradually to a point.

DISCUSSION. This species has hitherto been known only from the description by Tiner & Rausch (1950) who merely figured an *en face* diagram of the head. It appears in both sexes to be distinct in the structure of the head ; the male in the size of the spicule, in the size and shape of the gubernaculum, in the structure of the cloacal region, in the size and shape of the tail and in the number and structure of the mamelons.

Syphacia pallaryi (Seurat, 1915)

MATERIAL STUDIED. 4 ♂♂, 25 ♀♀ ex caecum of *Xerus getulus*. Agadir, Morocco.

MEASUREMENTS (in mm). See Table 3.

The head bears three, small, triangular lips (Pl. 2, fig. B).

Male. Two mamelons are present ; the post-cloacal papillae are pronounced (fig. 30) ; the spicule is of a medium length (fig. 32) ; the gubernaculum is characterised by the notches on the distal barb-like structure (fig. 33) ; the tail tapers rapidly to a short terminal spike (fig. 31).

Female. The vulva is protruded in both gravid and non-gravid specimens ; the non-gravid specimens have a brown cement-cap over the vulva (Pl. 3, fig. F) ; the musculature of the vagina is pronounced ; the eggs are of a medium size.

DISCUSSION. This species was initially described by Seurat (1915). It has since been redescribed once, by Chabaud & Biocca (1955), who compared it with *S. transafricana* from which it may be readily differentiated (see Discussion of *S. transafricana*, below).

Syphacia transafricana Chabaud & Biocca, 1955

MATERIAL STUDIED. 25 ♂♂, 25 ♀♀ ex caecum of *Xerus erythropus*. Dakar, French West Africa. Paratype-specimens.

MEASUREMENTS (in mm) See Table 3.

The anterior region of the body carries small cervical alae. The head bears three lips, which are reduced in size and appear to have an internal cuticular thickening (Pl. 2, fig. C).

Male. Two mamelons are present ; the post-cloacal papillae are not pronounced (fig. 34) ; the spicule is of medium size and tapers to a point distally ; the gubernaculum is complex and has an additional pair of lateral processes mid-way along the distal barb-like structure (figs. 35 & 36) ; the tail narrows suddenly at a level with the post-cloacal papillae and has a thin, terminal spike (fig. 34).

Female. The vagina is directed posteriorly and the vulva is not pronounced ; the eggs are of a medium size.

DISCUSSION. This species was initially described by Chabaud & Biocca (1955), who considered that it could be distinguished from *S. pallaryi* by the shape of the gubernaculum and the cloacal region of the male. Undoubtedly this species is similar to *S. pallaryi*, but the males may be readily differentiated from each other by the size of the spicule, by the shape and size of the gubernaculum, by the reduced size of the post-cloacal papillae and by the shape of the tail. Female specimens appear to be similar in most features, the protrusion of the vulva in specimens of *S. pallaryi* examined is not thought to be significant.

Syphacia thompsoni Price, 1928

MATERIAL STUDIED. 1 ♂, 3 ♀♀ ex *Glaucomys sabrinus macrotis*. Millestone, Jackson County, Wisconsin, U.S.A. B.M. (N.H.) Reg. Nos. 1951.12.14.149-151.

1 ♂, 2 ♀♀ ex *Glaucomys sabrinus*. Utah, U.S.A.

MEASUREMENTS (in mm). Only the first listed specimens have been measured.

Male. Body length 2.66 ; body-breath 0.141 ; diameter of head 0.047 ; oesophagus length 0.387 ; distance of mamelons from cloacal opening,—posterior 0.224,—middle 0.416,—anterior 0.658 ; length of spicule 0.187 ; length of gubernaculum 0.103 ; length of tail 0.312.

Females. Body-length 8.20, 9.07, 9.53 ; body-breadth 0.313, 0.311, 0.378 ; diameter of head 0.064, 0.061, 0.068 ; oesophagus length 0.521, 0.502, 0.551 ; distance of vulva from anterior end of body 1.39, 1.46, 1.37 ; length of tail 2.02, 2.29, 2.58.

The anterior end of the body has distinct cervical alae, which arise just behind the head and terminate approximately on a level with the middle of the oesophagus. The head bears three lips separated by interlabial grooves (Pl. 1, figs. E & F).

Male. Three mamelons are present ; the post-cloacal papillae are pronounced (fig. 38) ; the spicule is slightly curved and tapers rapidly to a point distally (fig. 38) ; the gubernaculum has the typical shape, but it is notched on the distal part, similar to that found in *S. emilromani* ; the tail tapers rapidly posterior to the post-cloacal papillae to form a long, thin, terminal spike.

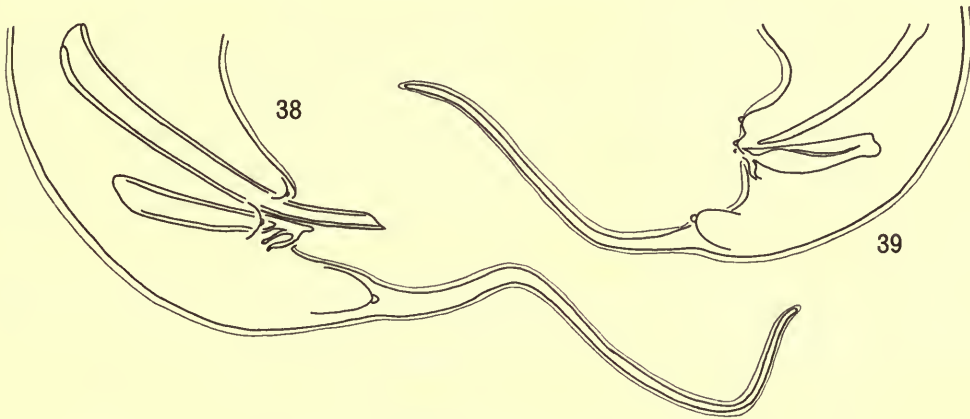
Female. None of the specimens examined are gravid ; the tail is long and tapers gradually to a fine point.

DISCUSSION. This species has been described previously from *Glaucomys v. volvans* by Price (1928) and from *Sciurus vulgaris* and *Sciurotamias davidianus* by Li (1933). In addition, Tiner & Rausch (1949) report the discovery of this species from the caecum of *Tamiasciurus hudsonicus*. However, as these specimens consisted of thirty-two males, but no females, they suggest that this infection is in an unnatural host.

The specimens described here agree in most respects with those previously described, although there appears to be an error in the length of the female tail as reported in the table of measurements by Li (1933). The author does not agree with the observation made by Schmidt & Kuntz (1968), that "... the specimens described

as *S. thompsoni* by Li (1933) represent an unnamed species", because the only differences between the two batches of material are in some measurements, whilst the morphological descriptions are very similar. It is possible that these differences in measurements may prove to be significant, but this can only be established by a comparison of the two sets of specimens.

This species is distinct in the structure of the head and in overall size ; in the male, the size and shape of the spicule and gubernaculum, the size of the cloacal papillae and the shape of the tail are its diagnostic features.



FIGS. 38-39. 38. Lateral view of male tail, *S. thompsoni*. 39. Lateral view of male tail, *S. pearsei*.

Syphacia pearsei Baylis, 1928

MATERIAL STUDIED. 3♂♂, 4♀♀ ex caecum of *Heliosciurus isabellinus*. Ase, Nigeria. B.M. (N.H.) Reg. Nos. 1929.I.24.22-24. Cotype and paratype specimens.

The anterior end of the body has cervical alae. The head bears three lips, each of which is separated by an interlabial groove (fig. 8).

Male. Two mamelons are present ; the spicule is of medium length, slightly curved and pointed distally ; the gubernaculum is complex ; the tail is long in the form of a slender terminal spike (fig. 39).

Female. The tail is long and tapers to a fine point.

DISCUSSION. This species has been described only once previously, from *Heliosciurus isabellinus*, by Baylis (1928). There appears to be nothing to add to the description of this species, except to remark on the structure of the head. The specimens of *S. pearsei* are equally preserved in spirit or as permanent slides, the former are in insufficient numbers to enable an *en face* examination, whilst the latter have unfortunately deteriorated and are not suitable for manipulation. Nevertheless, it appears that the structure of the head is similar to that of *S. thompsoni*, compare (figs. 7 & 8.)

This species is distinct in the structure of the head ; the male is distinctive in the size and shape of the spicule and of the gubernaculum, and in the form of the tail.

Syphacia eutamii Tiner, 1948

MATERIAL STUDIED. 2 ♂♂, 5 ♀♀ ex caecum *Eutamias minimus pictus*. Deep Creek Mts., Utah, U.S.A.

DISCUSSION. This species has already been adequately described by Tiner (1948). The additional observations reported here are those made possible by using the scanning electron microscope.

The head bears three lips, each of which is supported by a separate cuticular thickening. These thickenings are in the shape of the figure eight cut vertically in half, the middle arm of which is lengthened to connect with the apical region of each lip (Pl. 3, figs. A & B). An inner ring of six circumoral papillae is present.

The cuticle appears to have small vertical striations in addition to the typical transverse striations (Pl. 5, fig. A). In male specimens there are numerous, small, papilla-like structures (Pl. 4, fig. C) lying between the striations of the two ventral mamelons.

This species is distinct in the structure of the head ; the male is specific in the structure of the spicule and the gubernaculum, in the structure of the cloacal region, in the size of the tail and in the number and structure of the mamelons.

ACKNOWLEDGEMENTS

I am most grateful to Mr. S. Prudhoe, British Museum (Natural History), for his advice and criticism. I would also like to thank Prof. A. G. Chabaud of the Museum National d'Histoire Naturelle, Paris, and Dr. A. W. Grundmann of the University of Utah, U.S.A., for the loan of material.

TABLE I

Ratios and standard deviations for *Syphacia obvelata*, *S. emilromani*, *S. muris* and *S. stroma*.

The range and values for each ratio is shown by the bracketed figures.

	<i>S. obvelata</i>	<i>S. emilromani</i>	<i>S. muris</i>	<i>S. stroma</i>
males				
b	5.96 ± 0.43	6.58 ± 0.34	7.31 ± 0.54	5.24 ± 0.39
c	9.10 ± 0.93	9.01 ± 0.62	6.07 ± 0.47	9.28 ± 1.36
n	11	25	22	11
females				
b	12.93 ± 0.87	9.72 ± 0.57	11.28 ± 1.26	8.16 ± 0.94
c	6.03 ± 0.47	6.47 ± 0.49	6.59 ± 0.42	6.93 ± 1.11
V	12.7 ± 1.27	22.1 ± 1.24	23.9 ± 1.72	23.3 ± 2.27
n	25	25	25	25

b = length / length of oesophagus from anterior end ; c = length / length of tail ; V = length / distance of vulva from anterior end ; n = number of specimens.

TABLE 2

Measurements of *Syphacia obvelata*, *S. emilromani*, *S. muris* and *S. stroma*. (a) males (b) females. All measurements in mm.

	(a)			
	<i>S. obvelata</i>	<i>S. emilromani</i>	<i>S. muris</i>	<i>S. stroma</i>
Body-length	1.13-1.61 (1.35)	1.82-2.50 (2.15)	0.90-1.86 (1.42)	0.95-1.69 (1.22)
Body-breadth	0.131-0.172 (0.146)	0.099-0.145 (0.121)	0.052-0.148 (0.092)	0.068-0.153 (0.113)
Diameter of head	0.021-0.034 (0.029)	0.036-0.055 (0.040)	0.023-0.045 (0.033)	0.027-0.044 (0.035)
Oesophagus length	0.188-0.249 (0.226)	0.301-0.374 (0.327)	0.137-0.242 (0.193)	0.186-0.291 (0.234)
Distance of mamelons	0.132-0.209 (0.178)	0.161-0.383 (0.230)	0.112-0.195 (0.148)	0.120-0.166 (0.139)
from cloacal opening	0.268-0.374 (0.326)	0.387-0.729 (0.529)	0.230-0.370 (0.307)	0.242-0.303 (0.270)
Spicule-length	0.388-0.522 (0.462)	0.610-1.056 (0.781)	0.310-0.508 (0.427)	0.360-0.462 (0.401)
Gubernaculum-length	0.068-0.089 (0.078)	0.074-0.091 (0.080)	0.045-0.058 (0.053)	0.071-0.084 (0.078)
Length of tail	0.026-0.039 (0.034)	0.035-0.043 (0.039)	0.018-0.029 (0.025)	0.029-0.044 (0.036)
Number of specimens	0.122-0.172 (0.149) 11	0.199-0.242 (0.217) 25	0.135-0.308 (0.235) 22	0.101-0.148 (0.133) 11
(b)				
Body-length	3.72-5.61 (4.69)	3.61-4.89 (4.37)	2.72-4.34 (3.72)	2.12-3.77 (2.94)
Body-breadth	0.234-0.372 (0.316)	0.212-0.352 (0.270)	0.181-0.357 (0.288)	0.209-0.357 (0.289)
Diameter of head	0.036-0.050 (0.046)	0.044-0.058 (0.051)	0.036-0.056 (0.047)	0.041-0.057 (0.051)
Oesophagus length	0.329-0.431 (0.362)	0.364-0.497 (0.450)	0.249-0.416 (0.320)	0.288-0.435 (0.360)
Distance of vulva from anterior end of body	0.45-0.74 (0.59)	0.82-1.06 (0.96)	0.56-1.08 (0.89)	0.46-0.89 (0.68)
Length of tail	0.68-0.89 (0.78)	0.53-0.82 (0.68)	0.40-0.66 (0.56)	0.36-0.53 (0.43)
Range of egg size	0.099 × 0.036 to 0.118 × 0.041 25	0.068 × 0.034 to 0.085 × 0.038 25	0.066 × 0.030 to 0.091 × 0.043 25	0.128 × 0.039 to 0.148 × 0.046 25
Number of specimens				

TABLE 3

Measurements of *Syphacia montana*, *S. pallaryi* and *S. transafricana*. (a) males (b) females. All measurements in mm.

	(a)		(b)	
	<i>S. montana</i> = <i>obelata</i>	<i>S. pallaryi</i>	<i>S. transafricana</i>	
Body-length	1.33-1.77 (1.54)	1.43-2.21 (1.78)	1.32-1.63 (1.48)	
Body-breadth	0.121-0.148 (0.133)	0.139-0.234 (0.175)	0.084-0.119 (0.100)	
Diameter of head	0.030-0.036 (0.034)	0.025-0.032 (0.029)	0.017-0.023 (0.019)	
Oesophagus length	0.225-0.275 (0.243)	0.363-0.438 (0.397)	0.222-0.287 (0.247)	
Distance of mamelons	0.177-0.292 (0.228)	0.138-0.249 (0.211)	0.166-0.179 (0.173)	
from cloacal opening	0.385-0.590 (0.439)	0.278-0.604 (0.486)	0.324-0.360 (0.347)	
1.				
2.				
3.				
Spicule-length	0.413-0.817 (0.569)		0.065-0.077 (0.072)	
Gubernaculum-length	0.077-0.083 (0.081)	0.101-0.117 (0.107)	0.037-0.048 (0.041)	
Length of tail	0.036-0.041 (0.039)	0.065-0.069 (0.067)	0.088-0.116 (0.102)	
Number of specimens	0.159-0.197 (0.175) 5	0.106-0.121 (0.112) 4	25	
Body-length	3.24-4.99 (4.35)	2.90-3.92 (3.41)	2.27-3.09 (2.76)	
Body-breadth	0.172-0.279 (0.234)	0.228-0.345 (0.301)	0.151-0.302 (0.208)	
Diameter of head	0.037-0.058 (0.044)	0.027-0.043 (0.035)	0.026-0.036 (0.031)	
Oesophagus length	0.294-0.364 (0.344)	0.469-0.582 (0.523)	0.333-0.512 (0.373)	
Distance of vulva from	0.50-0.77 (0.64)	0.66-0.84 (0.76)	0.40-0.74 (0.59)	
anterior end of body				
Length of tail	0.55-0.89 (0.78)	0.39-0.64 (0.54)	0.29-0.49 (0.36)	
Range of egg size	0.104 X 0.30 to 0.122 X 0.047 25	0.072 X 0.028 to 0.091 X 0.033 25	0.065 X 0.026 to 0.087 X 0.038 25	
Number of specimens				

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PLATE 1

- A. Dorso-lateral view of head, *S. stroma*, $\times 1,500$
- B. *En face* view of head, *S. stroma*, lip-lobes slightly distorted, $\times 750$
- C. Dorso-lateral view of head, *S. peromysci*, $\times 1,500$
- D. *En face* view of head, *S. peromysci*, $\times 750$
- E. Dorso-lateral view of head, *S. thompsoni*, showing interlabial grooves, $\times 1,500$
- F. *En face* view of head, *S. thompsoni*, $\times 750$

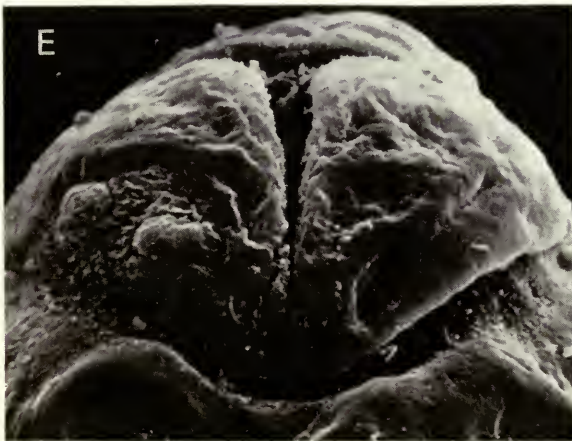
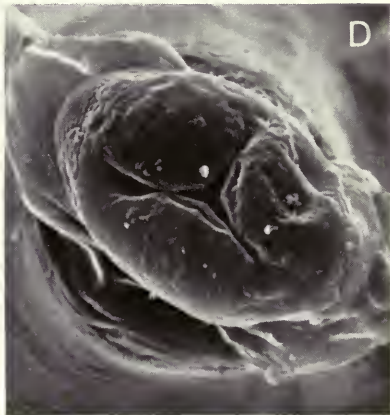
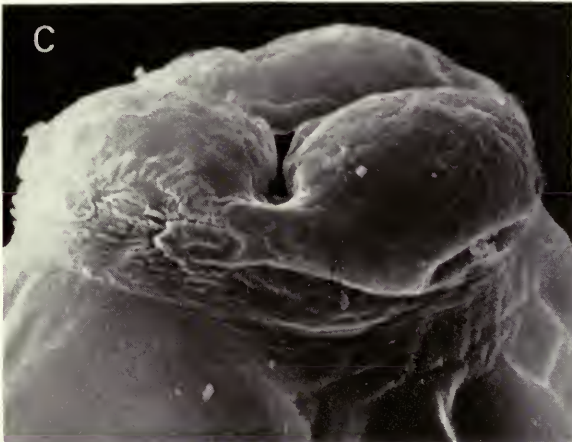
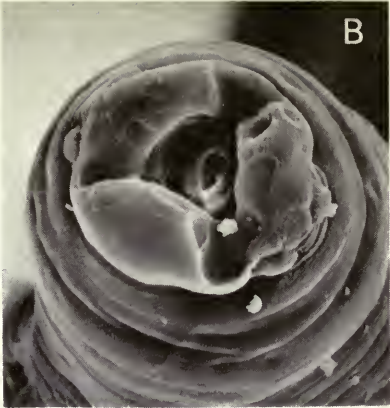
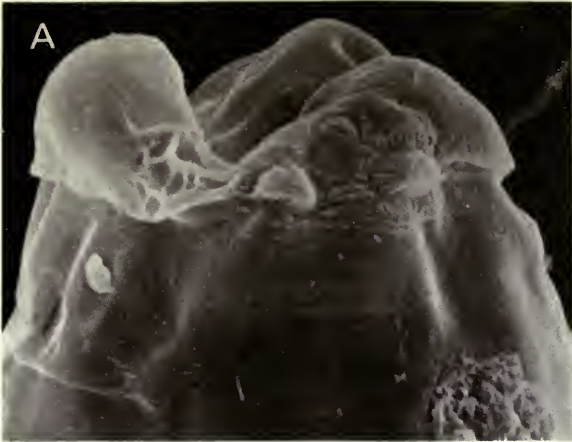


PLATE 2

- A. *En face* view of head, showing cuticular thickening, *S. citelli*, $\times 1,500$
- B. *En face* view of head, *S. pallaryi*, $\times 1,500$
- C. *En face* view of head, *S. transafricana*, $\times 1,500$

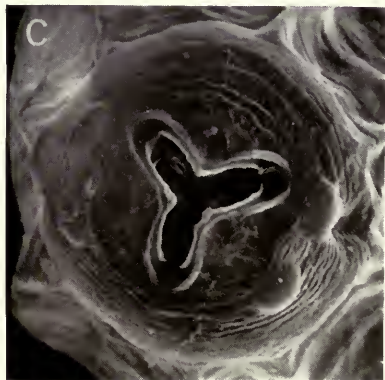


PLATE 3

- A. Dorso-lateral view of head, *S. eutamii* ; c, cuticular thickening, $\times 1,500$
- B. *En face* view of head, *S. eutamii* ; s, supporting septum, $\times 1,500$
- C. *En face* view of head, *S. emilromani*, $\times 1,500$
- D. Dorso-lateral view of head, *S. emilromani*, $\times 1,500$
- E. Lateral view of spicule projecting from cloacal opening, *S. obvelata*, $\times 2,800$
- F. Vulva of *S. pallaryi*, with partly detached cement-cap, cp. $\times 1,260$

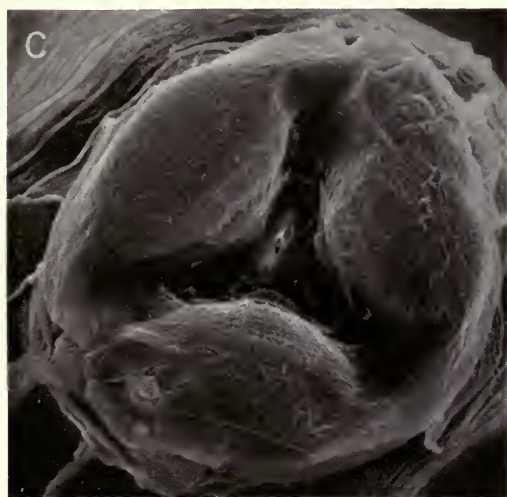
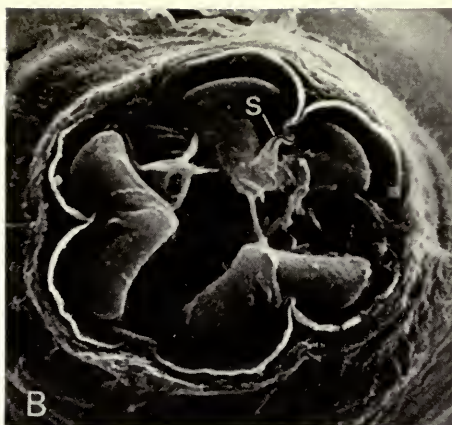
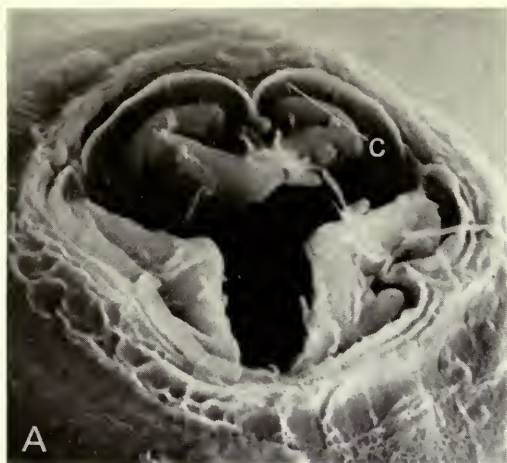


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- A. Lateral view of male, *S. peromysci*, showing three mamelons, m, and lateral line, l, $\times 140$
- B. Anterior mamelon of *S. stroma*, showing division of transverse ridge into two shallow elevations, $\times 1,000$
- C. Detail of papilla-like structures, *S. eutamii*, $\times 12,800$
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- E. Detail of papilla-like structures, *S. stroma*, $\times 21,000$

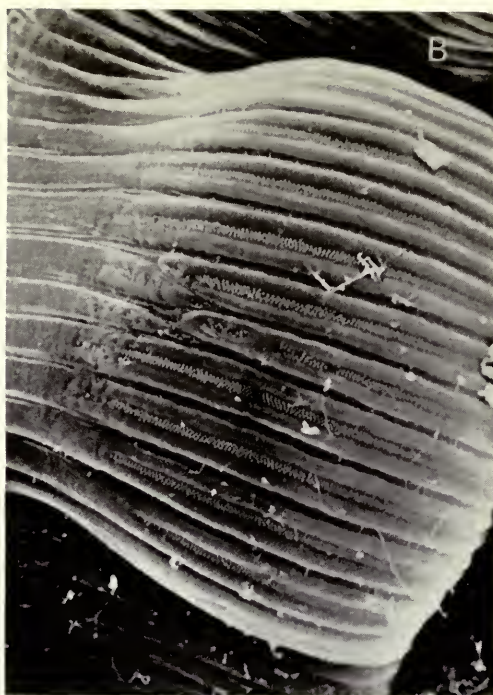
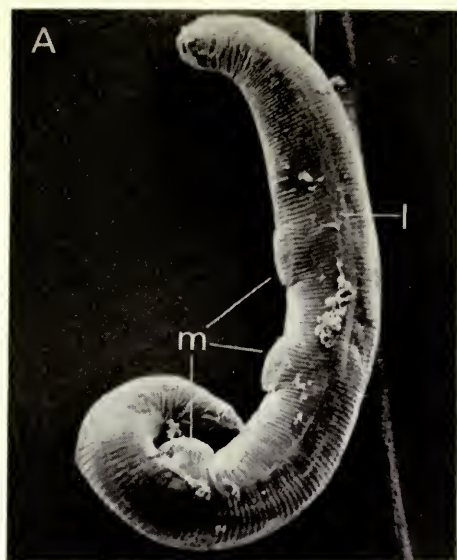
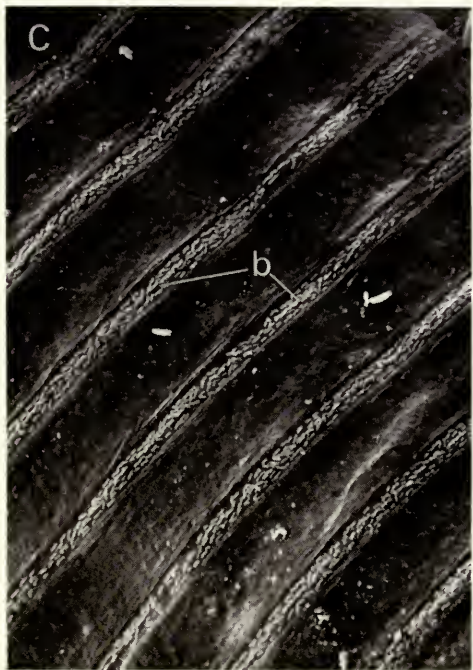


PLATE 5

- A. Cuticle of *S. eutamii*, showing transverse striations and small longitudinal ridges, $\times 2,100$
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Printed in Great Britain by
Alden & Mowbray Ltd
at the Alden Press, Oxford

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